A Monodominant Rain Forest on Maracá Island, Roraima, Brazil: Forest Structure and Dynamics.

A thesis submitted for the degree of
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by
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I hereby declare that this thesis has been composed by myself and except where otherwise stated the work contained herein is my own.

Marcelo T. Nascimento

To my parents and Dora

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ABSTRACT

A forest type dominated by *Peltogyne gracilipes* Ducke (Caesalpiniaceae) occurs on Maracá Island on a range of soil types. Maracá is located in Roraima State (Brazil) in the Rio Uraricoera and has an area of about 100,000 ha. This study compares the structure and floristic composition of the *Peltogyne* forest with the most widespread lowland forest type on Maracá and investigates some factors that could be involved in the persistent monodominance of *Peltogyne*. Three 0.25 ha plots were set up in each of three forest types: *Peltogyne*-rich forest (**PRF**), *Peltogyne*-poor forest (**PPF**) and forest without *Peltogyne* (**FWP**). Within each plot all trees (≥ 10 cm dbh) were recorded. Seedlings and saplings were sampled in sub-plots of 2 m x 1 m (seedlings) and 4 m x 4 m (saplings). In the **PPF** and **FWP**, Sapotaceae were the most important family with the highest dominance and relative density values. Caesalpiniaceae showed high values in the **PRF** and **PPF**. *Licania kunthiana*, *Pradosia surinamensis* and *Simarouba amara* occurred in the canopy layer in all the forest types. *Peltogyne* dominated the canopy in the **PRF** and had 20% of stems and 53% of the total basal area of all trees ≥ 10 cm dbh, and 91% of the stems and 97% of the total basal area of individuals > 50 cm dbh. In **PPF**, *Lecythis corrugata* and *Tetragastris panamensis* were the most abundant species, followed by *Peltogyne*. In the **FWP** the most abundant trees (≥ 10 cm dbh) were *L. kunthiana* and *P. surinamensis*. In general, *Peltogyne* had low rates of seed predation and herbivory, but suffered locally high levels of damage to its seeds by leaf-cutter ants and was once observed to have an infestation of larvae of the moth *Eulepidotis phrygionia* on its young leaves. *Peltogyne* had no allelopathic effects on tested species and had VA mycorrhizal associations. Its occurrence remains unexplained but is most clearly correlated with soil magnesium.

CONTENTS

Chapter 1. General introduction

INTRODUCTION

Studies on plant population dynamics are of prime importance for our understanding of ecological and evolutionary aspects of the natural tropical forest and also for its management (Wyatt-Smith 1987). Most tropical rain forests are very species-rich, but little is known of their dynamics (Manokaran & Kochummen 1987).

Long-term studies have been carried out on recruitment, growth and mortality of tree species (Lang & Knight 1983, Connell *et al.* 1984, Peralta *et al.* 1987, Manokaran & Kochummen 1987, Swaine *et al.* 1987, Martínez-Ramos *et al.* 1989). In the Amazon rain forest, long-term studies have been done in international co-operation projects. Maracá Island was one of the sites chosen for developing one of these projects (Maracá Rain Forest Project, INPA/SEMA/RGS) and since 1987 a long-term study on forest regeneration has been carried out there by J. Proctor.

The initial phase of field work on Maracá recorded a forest type dominated by *Peltogyne gracilipes* Ducke (henceforth usually referred to by its generic name only) of the Caesalpiniaceae, in which *Peltogyne* accounts for up to 75% of the basal area (Milliken & Ratter 1989). This forest type can be designated as monodominant, since by definition monodominant forests have one species with 50% to 100% dominance. As measures of dominance, the number of trees, basal area, biomass or canopy cover can be used (Connell & Lowman 1989). *Peltogyne* forests had already been mentioned by the explorer A. Hamilton-Rice (1928) reporting his expedition to Rio Branco, Uraricoera and Parima (1924-1925). He described a forest dominated by "pau roxo" (purple heart), the local name for *Peltogyne* referring to its spectacular purple heart-wood (Fig. 1.1), which occurs in a

Figure 1.1. The purple heart-wood of *Peltogyne*.

high number of trees of all sizes, especially near the banks of the Rio Uraricoera. He expressed his surprise at the dominance of "pau roxo" and emphasised that it is not common in Amazonia. According to RadamBrasil (1975) *Peltogyne* is a common species of the "Floresta Estacional Semidecidual" (semideciduous seasonal forest) in Roraima State, occurring in the regions of Rio Mucajaí, Serra Urucuzeiro, Serra Parima and Ilha de Maracá. Although there is no mention of the dominance of "pau roxo" as a forest type, the RadamBrasil (1975) considered that *Peltogyne* trees are clumped and form dense patches in some areas. It is noteworthy that although "pau roxo" was determined as *Peltogyne densiflora* (Hamilton-Rice 1928) and *P. lecointei* (RadamBrasil 1975), Lewis & Owen (1989) did not record these species in their survey of legumes of Maracá. According to them only two species of the genus occur on Maracá: *P. gracilipes* and *P. paniculata*. The former is common in riverine forest and hillsides, while the latter occurs often in the transition between forest and savanna (Ducke 1938, Silva 1976, Lewis & Owen 1989). Thus, the "pau roxo" reported by Hamilton-Rice (1928) and RadamBrasil (1975) is almost certainly *P. gracilipes*. Silva (1976), in her taxonomic review, mentioned that the geographical distribution of *P. gracilipes* is restricted to the Roraima State with this species occurring mainly on slopes and along the river Amajaí. Therefore, *Peltogyne* forests do not occur only on Maracá, but also on the mainland. A forest dominated by *Peltogyne* sp. (probably not *P. gracilipes*) was reported by Myers (1936) on sandy flood plains in British Guiana. According to him this forest type "forms, over limited areas, one of the purest stands of one tree species that I have ever seen". The Maracá *Peltogyne* forest seems to be the only reported case of a monodominant forest in the Amazon rain forest. However, elsewhere in Brazil monodominant plant communities are common, mainly in the "Pantanal" (i.e. swamp) area (Rizzini 1979, Nascimento & José 1986, Nascimento & Cunha 1990). Other types of monodominant

forests have been reported in many areas near Roraima such as the *Peltogyne* and *Mora* forests in British Guiana (Myers 1936), and the *Eperua* and *Monopterix* forests in Venezuela (Buschbacher 1984). All the species involved are legumes.

The occurrence of one or a few species dominating large areas of tropical forest was considered uncommon by Janzen (1970). However, monodominant rain forests have been noted in all regions of the tropics (Africa- Eggeling 1947, Gérard 1960, Swaine & Hall 1981; America- Marshall 1934, Beard 1946, Richards 1952, Buschbacher 1984, Milliken & Ratter 1989, Martijena & Bullock 1994; Asia- Whitmore 1984, Rai & Proctor 1986, Edwards *et al.* 1993, Swamy & Proctor 1995; Australia- Connell & Lowman 1989), but such single-dominant forests have seldom been studied by ecologists (Connell & Lowman 1989).

PROPOSED MECHANISMS FOR THE ORIGIN AND MAINTENANCE OF MONODOMINANT FORESTS IN THE TROPICS

A large number of studies have been published on the mechanisms maintaining high diversity among the canopy trees, such as compensatory mechanisms (Connell *et al.* 1984), predation and herbivory (Janzen 1970, Connell 1971) and perturbations (Hartshorn 1980, Pickett 1983, Brokaw 1985, Denslow 1987). On the other hand, little attention has been paid to low-diversity communities and only recently have attempts been made to explain the mechanisms that produce or maintain low-diversity among the canopy trees of tropical forests (Connell & Lowman 1989, Hart *et al.* 1989, Hart 1990). Many abiotic and biotic factors have been cited to lead dominance in a community, such as soil moisture regime or water-table level (Nascimento & Cunha 1989), soil nutrient concentrations (Richards 1952, Rizzini 1979), seed predation and herbivory (Boucher 1981), allelopathy (Gant & Clebsch 1975, Mabberley 1992) or ectomycorrhizas (Alexander

1989, Connell & Lowman 1989). In some cases, the occurrence of monodominance in a community may be related to a simple environmental stress. For example, the frequent occurrence of fires may promote dominance by a single fire-resistant species (Hart 1990) or waterlogging or periodical flooding may promote dominance by the exclusion of species unable to tolerate waterlogged conditions (Lieberman *et al.* 1985, Nascimento & Cunha 1990). However, monodominant forests also occur on well-drained soils and adjacent to species-rich forests where soils show similar characteristics. According to Connell & Lowman (1989) monodominant forests on well-drained soils can be produced by two ways:

1) the most common species produces abundant seed and dispersed them into a large open patch during the short period available before canopy closure;
2) the most common species gradually invades an existing diverse rain forest by tree-by-tree replacement.

Therefore, a monodominant species is likely to be the species most tolerant of adverse conditions and also the most efficient competitor for resources such as light, water or soil nutrients. Connell & Lowman (1989) recognised two types of monodominant forest:

Type I: with a persistent dominant which; once established, persists because of its abundant regeneration or its superior ability to exploit resources;

Type II: with a temporary dominant which does not persist beyond one generation, and shows poor recruitment in the understory because its seedlings cannot establish and survive after canopy closure. This type is related to an early successional process.

Hart *et al.* (1989) and Hart (1990) also recognised

these two types and similar mechanisms to those proposed by Connell & Lowman (1989) for the maintenance of the dominance. However, the hypotheses for the origin of the dominance were different. Connell & Lowman (1989) emphasized the importance of the ectomycorrhizal association in promoting type I dominance, while for Hart *et al.* (1989) and Hart (1990) the disturbance (or successional stage) was considered the key factor. According to Hart, type I forests occur where disturbance is infrequent and slight (late succession). In this case, the dominant species has lower seed predation and herbivory than the other species. Type II dominance occurs where disturbance is frequent and large (early succession) and so the dominant species shows poor recruitment in the understorey. In the case of intermediate disturbance (mid-succession) a species-rich forest is expected, with greater abundance of tree falls and shade-intolerant species.

THE AIMS OF THIS STUDY

The study of monodominant forests might improve our theoretical understanding of tropical species-richness by suggesting factors which might play an important role in species diversity in tropical forests. The *Peltogyne* forests occur on a wide range of soil types. Since fires are rare in the Maracá forests (Miller & Proctor 1994) it was decided that other abiotic and biotic factors should be investigated. A comparative study on the nutrient cycling in *Peltogyne* forest and forest without *Peltogyne* is being done by D. Villela. In this thesis I will deal with some abiotic (soil variables) and biotic factors such as seed predation, herbivory and occurrence of allelopathy, and ectomycorrhizal associations in *Peltogyne gracilipes*. This study will firstly describe the structure and floristic composition of a *Peltogyne* forest and its physical environment and compare

its features with other forest types on Maracá and in Amazonia. The following hypotheses will be tested:

1) the boundary between the *Peltogyne* and the surrounding species-rich forest is advancing or contracting;
2) the monodominant forest is prone to damage by herbivores (an environmentally less complex system should be prone to high level of herbivory, Brown & Ewel 1987), but the seedlings do not suffer mortality by density-dependent herbivory (Janzen-Connell model);
3) the *Peltogyne* has allelopathic effects on other tree species;
4) the *Peltogyne* has ectomycorrhizal associations ("Mycorrhiza hypothesis" of Connell & Lowman 1989).

Chapter 2. Maracá Island

LOCATION

Maracá Island is located between 3°15' and 3°35'N, 61°22' and 61°58'W in Boa Vista district, Roraima State, northern Brazil and it is formed by the splitting and rejoining of the Rio Uraricoera (Fig. 2.1). The Island is about 60 km long and 15-25 km wide and its area is about 100,000 ha. It is not river deposited, but part of the Northern Amazonian Dissected Plateau (RadamBrasil 1975). The Island has been protected by law from human interference since 1978 when it was established as the first ecological reserve of the Secretaria Especial do Meio Ambiente (SEMA). In 1989 with the abolition of SEMA, the Estaçao Ecológica de Maracá was transferred to IBAMA (Brazilian Environmental Institute).

PREVIOUS RESEARCH

Some published information about Maracá Island has been available for many years (eg. Koch-Grűnberg 1917; Hamilton-Rice 1928). Milliken & Ratter (1989) gave a brief summary of most of the studies (published and unpublished) from 1978 until the Maracá Rainforest Project (1987-1988). The most important was done, between 1980-1982, by Moskovits (1985) on tortoises. This study also provided data on the identity and flowering and fruiting phenology of the species which were important in the diet of *Geochelone* tortoises.

Since the Maracá Project, there have been many publications about the Island: four books (Hemming *et al.* 1988; Hemming 1994; Hemming & Ratter 1993 and Milliken & Ratter 1995), a special issue of *Acta Amazônica* (1991); and

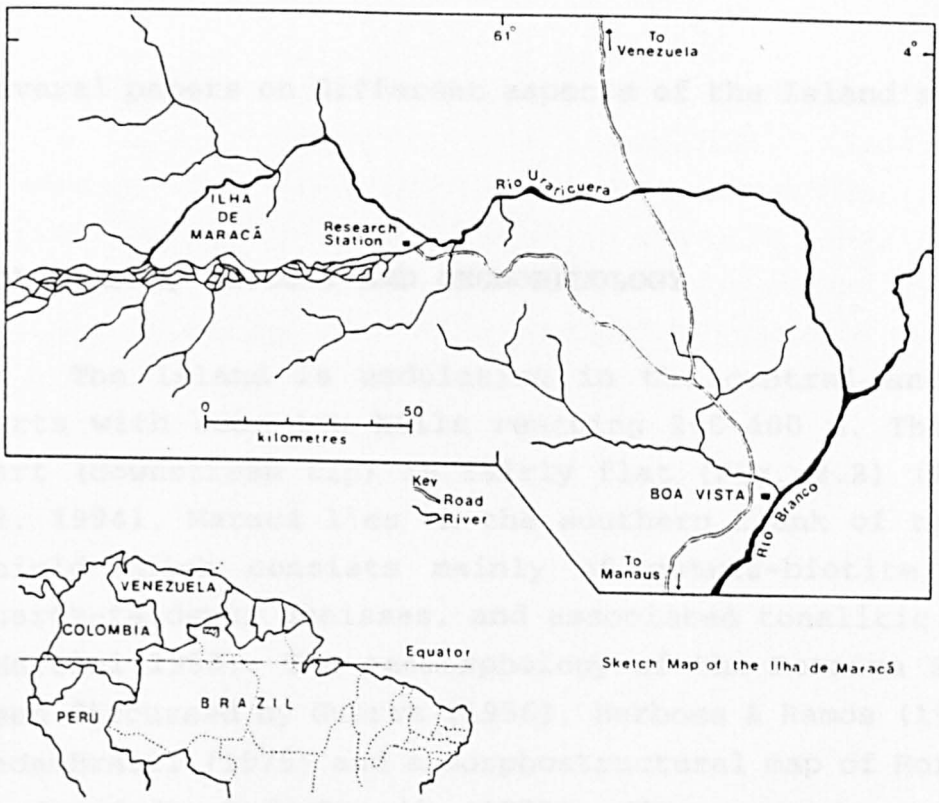


Figure 2.1. Location of Maracá Island.

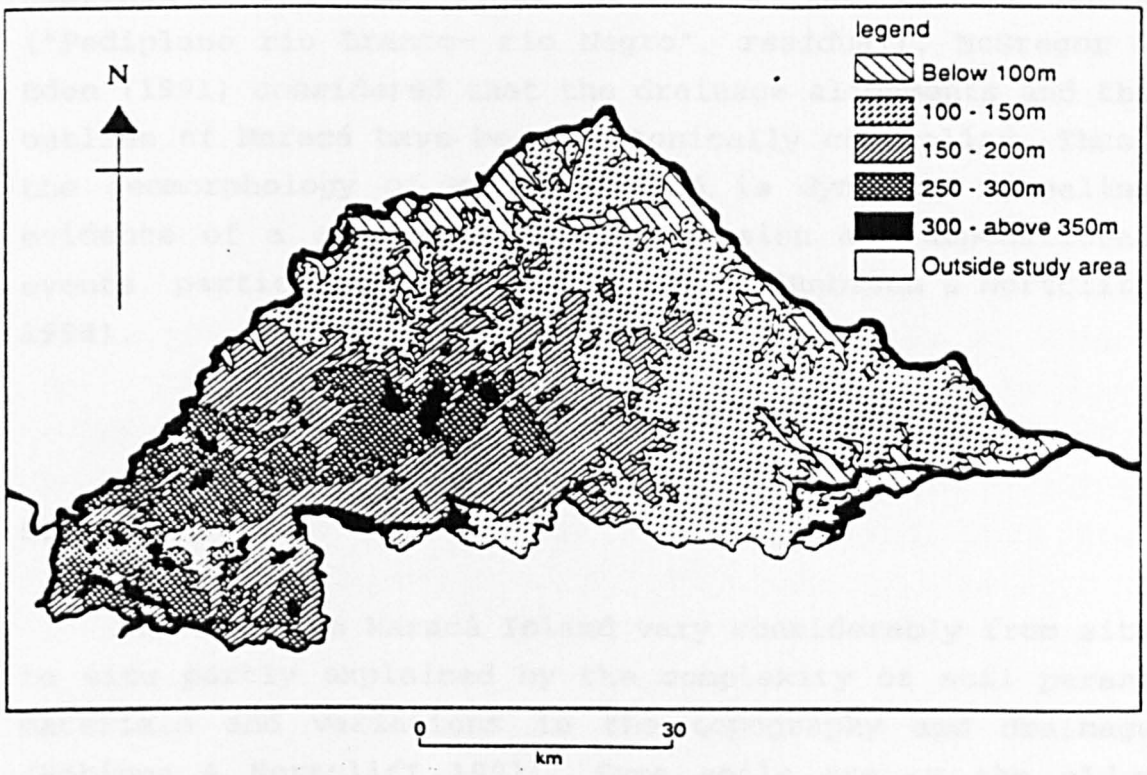


Figure 2.2. Topography of Maracá Island (from Furley *et al.* 1994).

several papers on different aspects of the Island's ecology.

TOPOGRAPHY, GEOLOGY AND GEOMORPHOLOGY

The Island is undulating in the central and western parts with some low hills reaching 200-400 m. The eastern part (downstream tip) is fairly flat (Fig. 2.2) (Furley *et al.* 1994). Maracá lies on the southern flank of the Guiana shield which consists mainly of quartz-biotite schists, quartz-feldspar gneisses, and associated tonalitic granites (Martini 1988). The geomorphology of the Roraima State has been discussed by Guerra (1956), Barbosa & Ramos (1959), and RadamBrasil (1975) and a morphostructural map of Roraima was produced by RadamBrasil (1975). This map shows that the eastern part of Maracá Island lies at the transition between the dissected high plain ("Planalto dissecado norte da Amazônia") and the lower areas of the Amazon basin ("Pediplano rio Branco- rio Negro", *residual*). McGregor & Eden (1991) considered that the drainage alignments and the outline of Maracá have been tectonically controlled. Thus, the geomorphology of Maracá Island is dynamic, revealing evidence of a complex series of erosion and depositional events, particularly in the Quaternary (Robison & Nortcliff 1994).

SOILS

The soils on Maracá Island vary considerably from site to site partly explained by the complexity of soil parent materials and variations in the topography and drainage (Robison & Nortcliff 1991). Some soils are on the older acidic residues (oxisols and ultisols), and other younger alluvial soils are on the more recent superficial deposits

(entisols and inceptisols). In the *Peltogyne* forest the soils are, according to Brazilian classification, predominantly "Podzólico amarelo distrófico plíntico" (Grossarenic Plinthic Paleudult in the USDA classification), dominantly "textura arenosa" with some "textura média", locally hydromorphic, with "Podzólico vermelho distrófico" on the low relief ridges and "Hidromórfico cinzento" in the wetter areas (Robison & Nortcliff 1991).

Information on the soils of the study sites is given in Chapter 4.

CLIMATE

Boa Vista, 130 km south of Maracá, has a high average annual temperature (26 °C), annual rainfall (1923-1988) of 1696 mm with a well marked dry season from October to March (Thompson *et al.* 1992a). According to Nimer's (1991) classification for the north region of Brazil, Maracá Island falls into the range of 1750 to 2000 mm annual rainfall. From 1989 to 1993 Maracá has had a mean annual rainfall of 1783 mm (source: Instituto Brasileiro do Meio Ambiente, IBAMA-RR). In general, the wettest month is July and the driest is February (Fig. 2.3). The dry season is more windy, with a predominance of the "Alisios" wind from NE (Nimer 1991). Temperature data collected on Maracá daily in a Stevenson screen in the field station clearing from 1 January 1991 to 31 December 1992 (Fig. 2.4) showed a similar pattern to that observed by Moskovits (1985) with mean monthly maxima ranging from 35.3 °C (June-July) to 40.7 °C (October-November) and mean monthly minima ranging from 22 °C (July) to 24.4 °C (May). The forests at the eastern part of the Island are located at the climatic transition between the savanna subtype (Aw) and monsoon subtype (Am) of the tropical rain climate (A) (Eidt 1968). Between 1989-1993, the number of months per year with less than 100 mm of

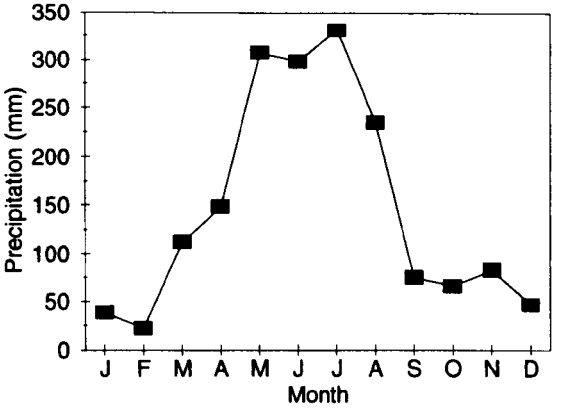


Figure 2.3. Mean monthly precipitation on Maracá Island from 1989 to 199

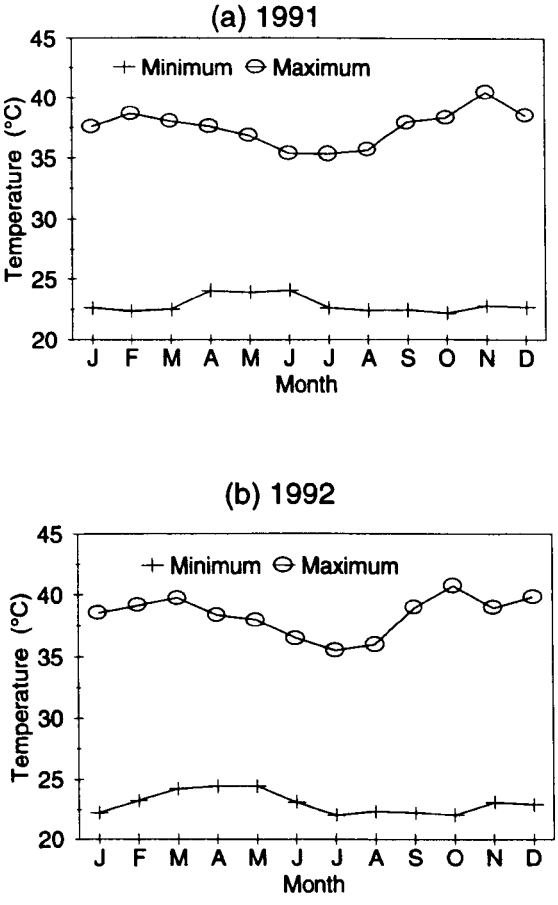


Figure 2.4. Mean monthly maximum and minimum temperatures in a Stevenson screen in the Field Station clearing in 1991 (a) and in 1992 (b) on Maracá Island, Brazil.

rainfall was six (September to February) with a total average rainfall of less than 100 mm giving a quotient of 0.50 if the seasonality is measured using the Schmit & Ferguson method (Whitmore 1984), that is the number of months with less than 100 mm to the number of months with more than 100 mm of rainfall. For Maracá this quotient falls into the seasonally dry category (Whitmore 1984). However, the dry season cannot be considered very strong since only December, January and February have less than 60 mm rainfall.

VEGETATION

Maracá is mainly covered with *terra firme* (meaning unflooded in Portuguese) forest (tropical lowland evergreen rain forest, *sensu* Whitmore 1984), with some areas of deciduous and semi-evergreen forests. According to Furley *et al.* (1994) the forests account for 84% of the Island (85,060 ha), with only small patches of savanna occurring at the eastern end of the Island which is at the zone of transition between the Amazonian rain forest and the Rio Branco-Rupununi savanna (Milliken & Ratter 1989).

Following the visit of the Maracá Rainforest Project in 1987-1988 several descriptions of the vegetation on Maracá have emerged, e.g. Milliken & Ratter 1989, Furley & Ratter 1990, Thompson *et al.* (1992a, 1992b, 1993). Milliken & Ratter (1989) classified the Maracá forests into six categories: *terra firme* forest of the eastern part of the Island; *terra firme* forest of the western part of the Island; *Peltogyne gracilipes* forest; low forest; buritizal and riverine forest. According to these authors the *terra firme* forest of the western hills shows a higher species richness than those of the east. The Euphorbiaceae are the most important family in the west and the Sapotaceae in the east. They highlighted the *Peltogyne* forest as rich in

biomass yet poor in diversity and meriting further study.

HUMAN OCCUPATION

Proctor & Miller (1995) have given archaeological, forest ecological, and historical evidence for the human occupation on the eastern part of Maracá Island. According to these authors, much of the *terra firme* forest in the eastern part of the Island was affected by Indian groups prior to their expulsion about 1880. Proctor & Miller (1995) did not include the *Peltogyne* forest in their account.

Chapter 3. Study sites and plots

THE FOREST TYPES

Three forest types were chosen according to the density of *Peltogyne*. Forests with a dominance of *Peltogyne* trees were designated as *Peltogyne*-rich forest (PRF), while forests with a sparse occurrence of this species were designated as *Peltogyne*-poor forest (PPF), and those with none, as forest without *Peltogyne* (FWP).

Maracá, as already mentioned, has about 84% of its area forested, of which 40% (34,136 ha) is semi-deciduous closed canopy forest (Furley *et al.* 1994), which corresponds to the tropical semi-evergreen rain forest of Whitmore (1984). According to the field data provided by Milliken & Ratter (1989), Nortcliff & Robison (1989) and this study, most of the semi-deciduous forests on Maracá can be considered as PRF or PPF, which cover about 30% of the island, most frequently in the central area. A map (Fig. 3.1) of forest distribution in the eastern part of the island was drawn based on the field information, satellite images taken from the Landsat thematic mapper in 1985 at the end of wet season (Milliken & Ratter 1989) and in 1992 in the dry season (IBAMA-DF), aerial photographs and personal notes from a flight on 12 April 1992 by micro-light plane, and from a vegetation map drawn by Jean Huffman (personal communication).

PRF forms strips, each up to several hundred hectares in area, which are conspicuous in the later part of the dry season when, from December to early April, many of the larger trees are leafless and so a sharp boundary can be seen between PRF and other forest types (Figs. 3.2 and 3.3).

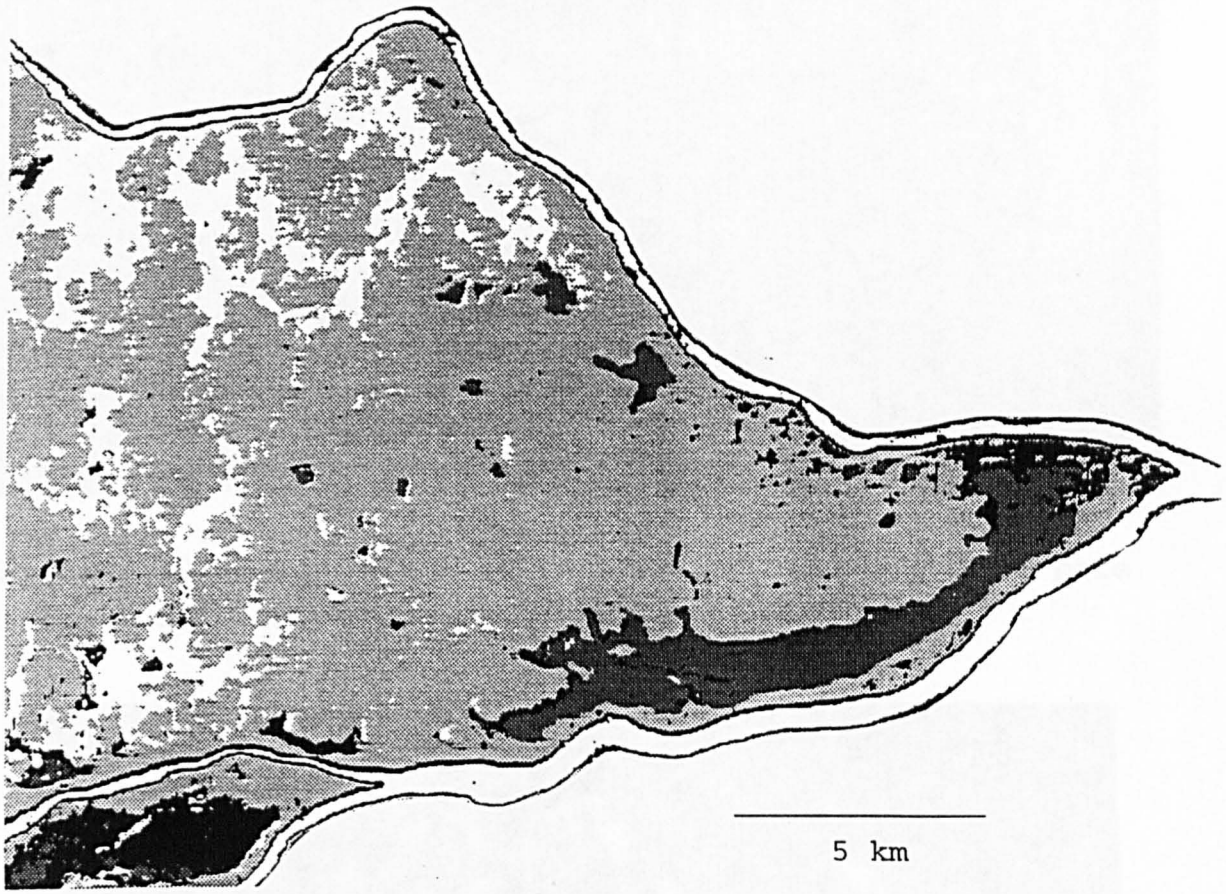


Figure 3.1. Distribution of the *Peltogyne* forests and forest without *Peltogyne* in the eastern part of the Maracá Island. On the island, white patches are *Peltogyne* forest, pale gray areas are FWP, and dark gray areas are savanna.

Figure 3.2. Aerial view of the PRF-FWP boundary. The pale areas are *Peltogyne* forest.

Figure 3.3. Close up of *Peltogyne* trees in the very early wet season (April 1992). During this period most tall *Peltogyne* trees were still leafless.

PLOT SELECTION

On 8-16 July 1991, three replicate plots of 50 m x 50 m were located in each of the three forest types. Plots 1-3 are in PRF, plots 7-9 in PPF and plots 10-12 in FWP (Fig. 3.4). All these plots were within an area of 4 km^2 near Trail 1 and the PRF in this area is called PRFa and the FWP in this area is called FWPa.

On 9-10 November 1991, another three plots (plots 4-6) were set up in another area of PRF (called PRFb) about 6 km south from the first one. These plots were located near each side of the river bank in the Furo Maracá very close to Maracá House (Fig. 3.4). Plot PRF 6 was located on a small island (2 ha) in the river. The plots were not seasonally flooded despite their proximity to the river, but they can be waterlogged in some years following exceptionally high rainfall.

The three unfelled plots (plots 3, 5 and 6) of Thompson *et al.* (1992a) of a FWP (called here FWPb) were given numbers 13-15 and included in the phytosociological and tree regeneration analyses.

The size of the plots was chosen according to Brűnig & Klinge (1976) who found that plots of about 0.25 ha were the most profitable in terms of time and information gained. The distances of the plots from the path (trail number 1 of the Maracá system, Milliken & Ratter 1989), were randomly chosen, except for the plots in PPF which had to be subjectively located close to the trail since this type of forest was rare.

Three transects (20 m x 180 m, each) were also set up in PRFa (Fig. 3.4). The distance between transects 1 and 2 was 133 m, between 1 and 3 113 m, and between transects 2 and 3 266 m.

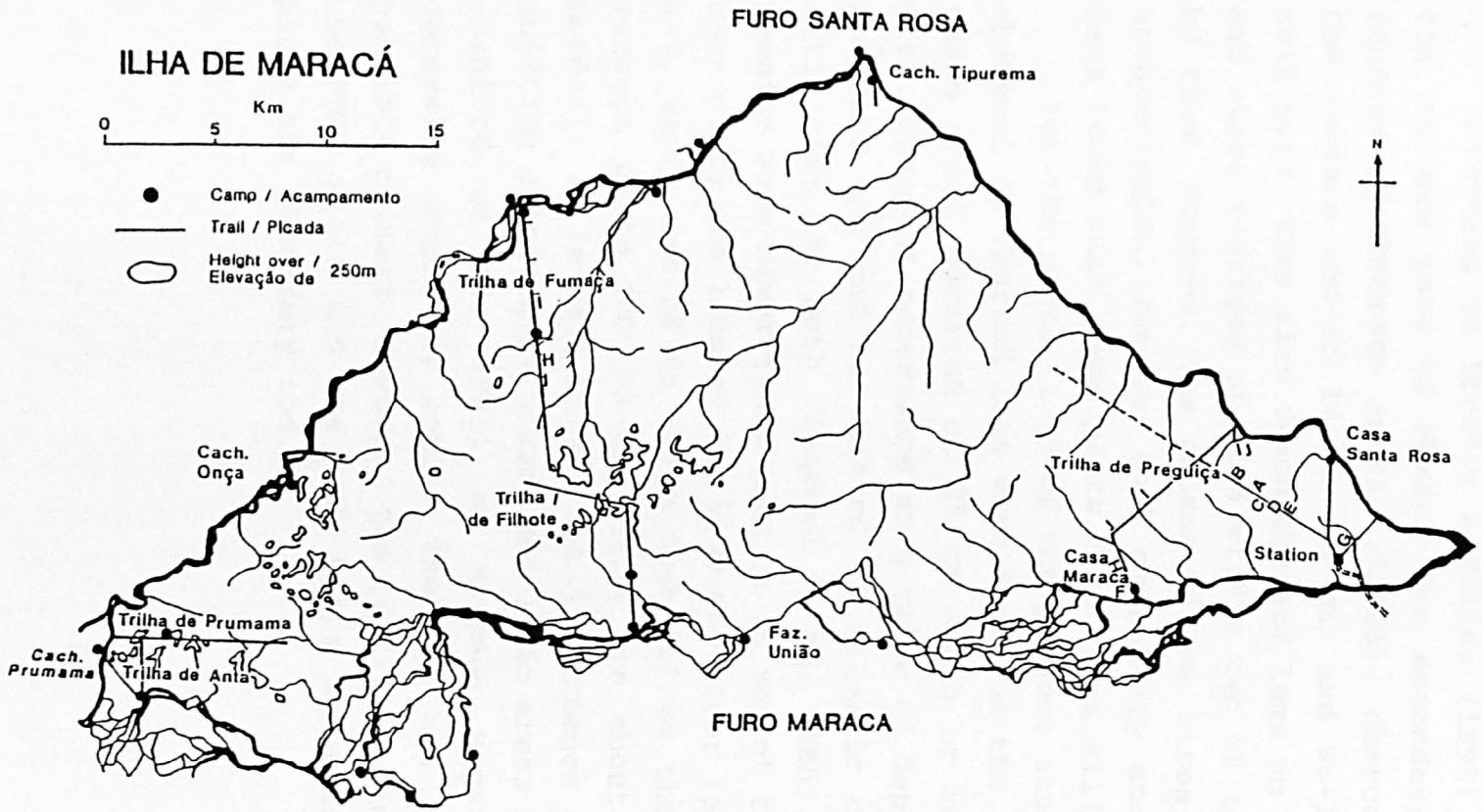


Figure 3.4. The location of the study forests (A, PRFa; B, PPF7; C, PPF8; D, PPF9; E, FWPa; F, PRFb; and G, FWPb) and other areas of PRF (H, Milliken & Ratter 1989 and I, Robison & Nortcliff 1991) and PPF (J, Robison & Nortcliff 1991) on Maracá Island. The distances from the base camp to the plots in each forest type are about 1000 m (FWPb plots 13-15), 3400 m (FWPa plots 10-12); 3850 m (PPF9); 4650 m (PPF8); 4800 m (PRFa plots 1-3); 5800 m (PPF7) and 8000 m (PRFb plots 4-6). Transects 1-3 are located in A (PRFa).

HUMAN DISTURBANCE OF THE PLOTS

According to Proctor & Miller (1995) most forests in the eastern part of Maracá are secondary. In the plots studied by Thompson *et al.* (1992a), charcoal was found on the surface and at 10 cm, 20 cm, and 50-100 cm depths in soil pits. They also found charred logs on the soil surface and other vestiges of fire within two of the plots studied by them. However, the causes of the fires remain unknown. Archaeological remains such as pottery and stone axeheads were found near these plots (Proctor & Miller 1995).

For the plots (1-12 of the present study), no signs of charcoal or charred logs were found on the soil surface but these often occurred at 25 cm depth or more in the soil pits. Charcoal occurrence at a range of depths is common in Amazonia and can be related to climatic changes or human activities, or both (Sanford *et al.* 1985). Archaeological remains were never found near or in any of the plots (1-12). Most plots are located far from the river (except plots PRFb 4-6, which are 20 to 100 m from it) or the savanna border (except plots FWP 13-15, which are about 1 km from the border). It is well known that disturbance of the forest by shifting cultivators occurs mainly in areas bordering rivers (Sanford *et al.* 1985) or savanna vegetation, but is generally small in scale. The PRF and PPF studied are possibly primary. However, the floristic similarity between the FWPa plots and the FWPb plots suggests that the FWPa plots are secondary too.

Chapter 4. The soils, forest structure and floristic composition of the study plots

INTRODUCTION

The structure and floristic composition of the Amazonian lowland rain forest has been studied in several areas in Brazil (Black *et al.* 1950; Takeuchi 1961; Prance *et al.* 1976; Campbell *et al.* 1986, Prance 1990; Rankin-de-Merona *et al.* 1992; Thompson *et al.* 1992a; Almeida *et al.* 1994); Bolivia (Boom 1986); Ecuador (Balslev *et al.* 1987, Valencia *et al.* 1994); Peru (Gentry 1988) and Venezuela (Uhl & Murphy 1981, Buschbacher 1984). These authors have shown that the number of tree species ≥ 10 cm diameter at breast height (dbh) per hectare in the lowland evergreen rain forests varies from about 80 for forests which are seasonally dry to about 300 for the forests, without a dry season, and which are perhaps the most species-rich in the world (Gentry 1988). Contrary to the previously widespread view (e.g. Whitmore 1984), Gentry (1988) showed that some Amazonian tree communities may be more diverse than the South-east Asian dipterocarp forests. However, this conclusion was based on a few sample plots. Sample plots in FWP at the eastern Maracá island had only 84 species per 1.5 ha (Thompson *et al.* 1992a). Maracá is located at the zone of transition between the Amazonian rain forest and the savanna and according to Gentry's (1988) classification could be considered a lowland dry forest. On the other hand, Thompson *et al.* (1992a) considered that the evergreen forests on Maracá should be classified as a lowland evergreen tropical rain forest according to Whitmore's classification (1984) or as an evergreen seasonal forest (Beard's classification 1944).

Although Milliken & Ratter (1989) for vegetation, and Nortcliff & Robison (1989) for soils, provided some data for PRF on Maracá, no detailed or comparative studies have been

done on its ecology. Connell & Lowman (1989) pointed out that although monodominant tropical rain forests have been recorded in several parts of the world (Chapter 1), they have seldom been studied by ecologists.

This Chapter describes and compares the soils, structure and species composition of the PRF, PPF and FWP.

METHODS

SOIL SAMPLING AND ANALYSIS

A soil pit was dug in the middle of plots 1-3 (PRFa), 7-9 (PPF) and 10-12 (FWPa) (Chapter 3). The soil profiles were described according to Hodgson (1978) and soil samples were collected from each horizon in March 1992. Each soil sample was air-dried and sieved through a 2-mm mesh and 150 g subsamples were stored for up to six months in air-tight polythene bags until shipment to the University of Stirling for analysis. Soil descriptions for the other plots were taken from Thompson *et al.* (1992) (FWPb) and Nortcliff & Robison (1988) (PRFb).

Chemical analysis followed Thompson *et al.* (1992a). Loss-on-ignition was determined on oven-dried samples after heating at 375 °C for 16 h. pH was measured in a 1:2 soil:deionized water mix which was stirred and allowed to stand for 1 h. Total nitrogen and phosphorus were extracted from 1.0-g subsamples of soil digested in a mixture of 4.4 ml of the mixed digestion reagent (420 ml of concentrated sulphuric acid, containing 0.1% selenium as a catalyst, and 350 ml of "100 volume" hydrogen peroxide). They were measured colorimetrically by a FIAstar 5010 flow injection auto-analyser using the gas diffusion method (FIAstar application sheet no. 50-03/84) for nitrogen and the stannous chloride-ammonium molybdate method (FIAstar application sheet no. 60-02/83) for phosphorus. For analysis

of exchangeable cations, 10-g subsamples of soil were extracted by 10 successive additions of 10 ml of 1 M ammonium acetate solution adjusted (by the addition of acetic acid) to pH 4.9 and were determined on a Varian AA-575 Atomic Absorption Spectophotometer using an air-acetylene flame for sodium and potassium and a nitrous-oxide-acetylene flame for calcium and magnesium. Total acidity and exchangeable aluminium were analysed by titration after 10-g subsamples of soil were leached by ten successive additions of 10 ml of 1 M potassium chloride solution. Total acidity was measured by titration with NaOH using phenolphthalein as the indicator. Another titration with 5 mM hydrochloric acid was carried out for exchangeable aluminium, after adding 10 ml of 1 M potassium fluoride to the titration solution. Hydrogen was estimated as the difference of the total acidity and aluminium. The sum of total exchangeable cations plus total acidity were calculated to determine the values of cation exchange capacity. Particle-size composition was measured using the hydrometer method (EMBRAPA 1979) on 50-g soil samples from each soil pit sample.

Soil surface (0-10 cm) samples were collected from the middle of each of 10 randomly selected 10 m x 10 m subplots within plots 4-6 of PRF on 7 July 1992. Surface soil data from plots FWP 10-12; PPF 7-9 and PRF 1-3 were provided by D. Villela (unpublished) from samples collected, in the same way as those described earlier, on 29-30 June 1992 (wet season). For these soil samples, extractable nitrogen and phosphorus rather than total nitrogen and phosphorus were analysed. For the plots FWP 13-15, data were used from Thompson *et al.* (1992a) for soil samples collected on 28 June 1987.

FLORISTIC INVENTORY

Within each plot the diameter of all trees and lianas

≥ 10 cm dbh were recorded between September and November 1991 and they were marked with permanent aluminium tags. For trees with large buttresses or prop roots reaching more than 1.3 m high the diameters were measured at 30 cm above these protrusions. In each plot of PRFa, PPF and FWPa, all trees were checked for the presence of lianas, but only trees that had one or more lianas climbing their trunks, and not merely crossing from the crowns of adjacent trees, were considered as liana supporters. Only lianas ≥ 10 cm dbh were identified. Standing dead trees and fallen trunks (dbh ≥ 10 cm) were also recorded. For trees with multiple stems, each stem was measured separately and the tree basal area was considered as the sum of the basal area of each stem (which was ≥ 10 cm dbh). During the enumeration, each tree was identified as far as possible and confirmed from collected specimens. Voucher specimens are lodged in the Herbarium of Instituto Nacional de Pesquisas da Amazônia (INPA, Manaus, Brazil) and the Herbarium of the Royal Botanic Gardens, Edinburgh (Scotland). Most of the infertile specimens are also in the Herbarium of Museu de Ciências de Roraima (Boa Vista, RR, Brazil).

A profile diagram of trees over 6 m tall was made for one plot in each forest type using a 60 m x 7.5 m transect (of which 50 m was within one of the sample plots). The height of each tree was estimated by comparison with an 8 m pole and independent estimates were made for each tree by two persons and the average value used. Heights (trees > 20 m tall) were later confirmed with a Haga gauge.

Seedlings (≤ 0.5 m in height) and saplings (> 0.5 m height, < 10 cm dbh) were sampled in five subplots of 2 m x 1 m (seedlings) and 4 m x 4 m (saplings). These subplots were located in a stratified random way within each of the forest plots. The density of herbs and small palms was also recorded from the 4 m x 4 m subplots.

DATA ANALYSIS

Soil data

Among-forest-type comparisons of the surface soil data were made by two-way nested ANOVA where factor A (forest type) was considered fixed and factor B (plots) random. If significant differences among levels of a factor occurred they were checked using a Tukey test (Zar 1984).

Vegetation data

The data were analysed using the FITOPAC package designed for PC computers by George Shepherd (Department of Botany, University of Campinas, São Paulo, Brazil). Relative density (RD) and relative dominance (RDo) of each family or species were calculated according to the formulae of Cottam & Curtis (1956): $RD = 100\ n_i/N$, $RDo = 100\ (BA_i/BA)$; where n_i = the number of individuals of the family i or species i, N = total number of individuals, BA_i = basal area of the family i or species i, BA = total basal area. The cover value index (CVI) of Förster (cited in Oliveira-Filho *et al.* 1989) for each species and family was calculated by summing the relative values of density and dominance. This index was considered most suitable to rank the families and species as equal weighting is given to density and basal area.

Family similarity between each forest type was calculated using the Sørensen coefficient (Brower & Zar 1977), CCs= 2c/(a+b), where c is the number of families common to both sites; a= the number of families on site 1; b= the number of families on site 2). For species similarity a quantitative index (Morisita's index) was used (Brower & Zar 1977):

$Im = 2 \sum X_i.Y_i/(A+B)N_x.N_y$, where $A = X_i(X_i-1)/N_x(N_x-1)$ and $B = Y_i(Y_i-1)/N_y(N_y-1)$;

X_i is the number of individuals of species i in community X, Y_i is the number of individuals of species i in community Y. N_x is the total number of individuals in community X and N_y is the total number of individuals in community Y. This index is based on Simpson's index of dominance and according to Brower & Zar (1977) refers to the probability that individuals randomly drawn from each of the two communities will belong to the same species, relative to the probability of randomly selecting a pair of specimens of the same species from one of the communities. Both Sørensen's coefficient and Morisita's indices, vary between 0 and 1 and values higher than 0.5 mean high similarity between communities.

Species diversity was measured using two indices: the Shannon index ($H' = -\sum p_i \ln p_i$, where $p_i = n_i/N$ and n_i is the number of individuals of species i and N is the total number of individuals), and Simpson's index ($Ds = 1-\sum(n_i(n_i-1)/N(N-1)$ (Brower & Zar 1977). The Shannon index assumes that individuals are random sampled from an "indefinitely large" population and that all species are represented in the sample (Magurran 1988). Shannon index values are usually between 1.5 and 3.5 and only rarely surpass 4.5 (Margalef 1972). According to Taylor (1978), they are usually normally distributed when a number of replicates have been taken and therefore it is possible to apply parametric statistics to compare them. The Simpson index is, as the Shannon index, based on the proportional abundances of species. The former index is more affected by rare species while the latter is sensitive to a shift in the dominance of the species (Peet 1974).

Since one of the main aims of this study is to investigate the effect of the dominant *Peltogyne* on the other canopy species, the diversity indices for the PRF plots were also calculated excluding data for *Peltogyne*. In this case if the forest types had initially the same total tree density, the number of canopy trees in PRF would be less than in PPF and FWP.

A oneway ANOVA was used to compare the mean diversity values among forest types and a Tukey test was used for the multiple comparison (Zar 1984). Rank-abundance diagrams (Begon *et al.* 1990) for the first 10 most abundant species were plotted for each forest type. Species-area curves were drawn for each plot of each forest type. All the analyses, except the rank-abundance diagrams and species-area curves, were carried out separately for trees with dbh ≥ 10 cm, ≥ 30 cm, and ≥ 50 cm.

RESULTS

SOIL PITS

A description of each soil pit is given in Appendix 1. Figure 4.1 shows a profile pit in PRFa and Fig 4.2 a pit in FWPa. Chemical and textural data for each pit are shown in Table 4.1. The soils had neither a surface organic horizon nor a root mat. They were in most cases very sandy and well drained. All soils were poor in nutrients but not podzolized. PRFa soils were always richer in magnesium than FWP and had high values of the Mg/Ca quotient, especially in the deepest horizons.

SURFACE SOILS

Soil chemical and particle-size composition from surface soils are shown in Table 4.2. In all forest types, the surface soils had similar characteristics. They were sandy and acid with low concentrations of total phosphorus and exchangeable cations. However, PRF and PPF soils had in general the highest concentrations of exchangeable cations, especially for magnesium, with the highest Mg/Ca quotients and Mg/total base quotients occurring in PRF. PRF had less

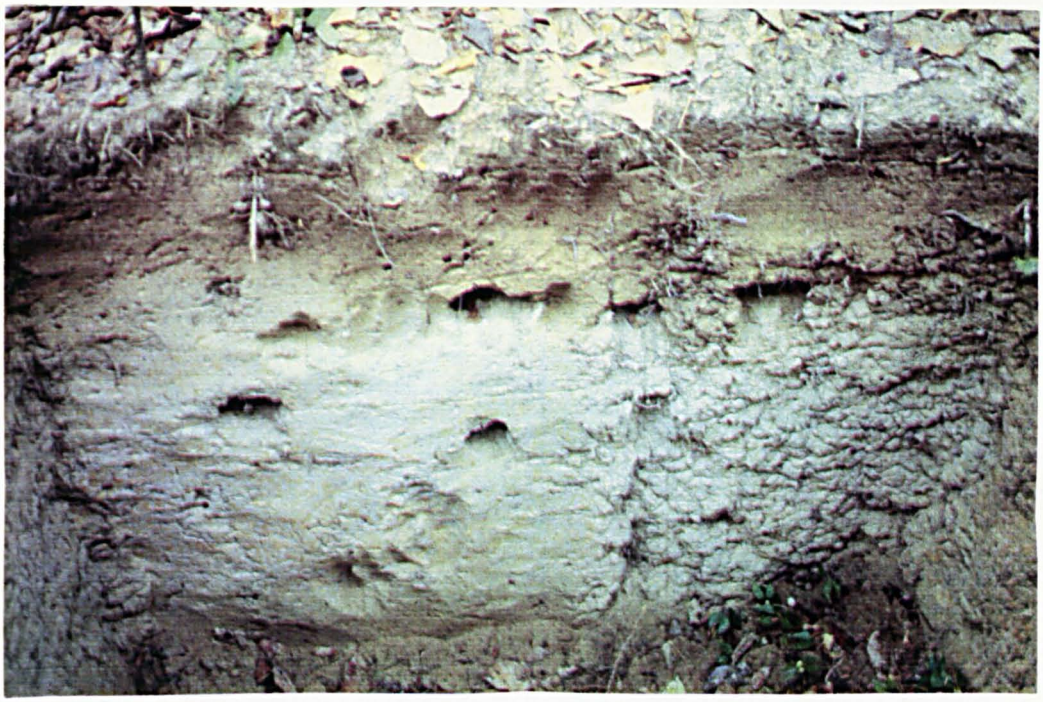


Figure 4.1. A view of the soil profile at plot PRF2 on Maracá Island, Brazil.

Figure 4.2. A view of the soil profile at plot FWP11 on Maracá Island, Brazil.

Table 4.1. Soil chemical properties and particle size composition from each soil horizon depth from each plot in three different forest types on Maracá Island, Brazil. PRF= *Peltogyne*-rich forest, PPF= *Peltogyne*-poor forest and FWP= forest without *Peltogyne*.

Horizon depth (cm)	pH	Loss. ign. (%)	Ntotal mg/g	Ptotal µg/g	K+	Na+	Ca2+	Mg2+	total acidity	Al+++	H+	CEC	Mg/Ca	Base (%)	Clay (%)	Silt sat. (%)	Sand (%)
					mequiv.kg^{-1}												
PRF1																	
0-13	4.7	2.26	0.76	86	1.54	0.11	2.96	2.77	8.7	3.1	5.6	16.1	0.9	45.8	13	15	72
13-39	4.8	0.83	0.29	77	0.57	0.05	0.28	1.11	11.0	4.6	6.4	13.0	4.0	15.4	14	15	71
39-86	5.1	0.32	0.09	52	0.53	0.07	0.27	0.95	7.2	3.3	3.9	9.1	3.5	20.1	14	15	71
86-134	4.9	0.51	0.18	75	0.31	0.11	0.11	1.54	12.5	6.1	6.4	14.6	14.0	14.2	15	13	72
PRF2																	
0-10	4.9	1.67	0.61	90	1.07	0.04	1.90	1.66	9.0	4.4	4.6	13.7	0.9	34.2	14	14	72
10-35	5.0	1.21	0.38	83	0.63	0.04	1.08	0.95	8.5	5.0	3.5	11.2	0.9	24.1	15	14	71
35-62	5.1	0.70	0.23	69	0.54	0.10	0.49	0.99	7.5	5.1	2.4	9.6	2.0	22.0	16	12	72
62-120	5.0	0.52	0.15	61	0.50	0.21	0.25	2.76	7.0	4.2	2.8	10.7	11.0	34.7	18	11	71
PRF3																	
0-9	4.5	3.27	0.78	92	1.58	0.07	0.98	2.21	13.0	8.5	4.5	17.8	2.2	27.1	24	13	63
9-28	5.2	2.28	0.46	78	1.65	0.09	0.20	0.65	10.7	7.9	2.8	13.3	3.2	19.4	27	13	60
28-49	4.9	1.72	0.38	67	0.90	0.08	0.16	0.63	11.0	8.0	3.0	12.8	3.9	13.9	47	10	43
49-134	5.0	3.88	0.25	43	0.96	0.10	0.45	4.18	11.2	8.4	2.8	16.9	9.3	33.6	55	12	33
PPF7																	
0-15	4.6	1.80	0.43	36	0.86	0.05	0.85	0.93	5.2	3.9	1.3	7.9	1.1	33.9	16	10	74
15-28	4.5	1.35	0.45	43	0.91	0.05	0.40	0.85	6.5	5.3	1.2	8.7	2.1	25.4	27	13	60
28-51	4.8	3.02	0.35	36	1.48	0.06	0.33	1.52	8.2	6.3	1.9	11.6	4.2	29.2	56	10	34
51-141	5.0	4.95	0.27	25	1.44	0.09	0.38	1.39	10.2	8.1	2.1	13.5	3.7	24.4	55	10	35
PPF8																	
0-9	4.8	2.06	0.49	67	0.77	0.05	0.58	0.94	6.2	5.4	0.8	8.6	1.6	27.3	18	10	72
9-22	4.9	1.94	0.41	63	0.50	0.04	0.25	0.48	7.0	5.2	1.8	8.3	1.9	15.3	29	12	59
22-56	5.1	2.70	0.29	49	0.69	0.08	0.13	0.47	7.7	6.6	1.1	9.1	3.6	15.1	42	11	47
56-103	4.9	4.61	0.33	39	0.58	0.10	0.26	1.84	10.0	7.9	2.1	12.8	7.1	21.8	50	12	38
PPF9																	
0-8	4.6	6.67	0.54	56	1.83	0.07	1.33	2.01	5.2	3.4	1.8	10.5	1.5	49.9	17	12	71
8-47	5.0	1.76	0.33	41	0.93	0.05	0.68	0.82	7.2	6.3	0.9	9.7	1.2	25.5	20	14	66
47-135	5.1	3.78	0.28	28	0.85	0.07	0.80	0.58	14.0	11.8	2.1	16.3	0.7	14.1	43	12	45
FWP10																	
0-15	4.6	0.71	0.25	25	0.37	0.08	0.33	0.27	3.5	2.2	1.3	4.6	0.8	23.2	11	11	78
15-33	4.8	0.93	0.22	33	0.21	0.06	0.03	0.11	4.5	3.8	0.7	4.9	3.7	8.4	14	13	73
33-72	4.7	0.51	0.15	27	0.25	0.04	0.04	0.11	5.5	5.0	0.5	5.9	2.7	7.4	16	11	76
72-148	4.6	1.40	0.13	26	0.25	0.05	0.02	0.07	6.2	5.6	0.6	6.6	3.5	5.6	23	8	69
FWP11																	
0-16	4.6	1.94	0.44	40	1.23	0.08	0.94	1.23	4.5	4.0	0.5	8.0	1.3	43.6	16	7	77
16-49	4.7	1.77	0.26	31	0.89	0.06	0.25	0.35	7.5	6.7	0.8	9.0	1.4	17.1	19	8	73
49-97	4.6	1.78	0.99	28	0.61	0.06	0.32	0.30	8.0	6.9	1.1	9.3	0.9	13.9	20	11	69
97-140	4.5	3.22	0.19	28	0.59	0.06	0.05	0.18	10.7	9.9	0.8	11.6	3.6	7.5	3	9	61
FWP12																	
0-15	4.7	1.31	0.32	29	0.51	0.05	0.28	0.40	4.2	2.7	1.5	5.5	1.4	22.7	16	11	73
15-35	4.7	1.46	0.26	30	0.60	0.07	0.07	0.21	5.7	5.3	0.4	6.7	3.0	14.2	19	11	70
35-84	4.6	1.59	0.18	27	0.42	0.05	0.17	0.21	6.2	5.4	0.8	7.1	1.2	12.0	20	11	69
84-146	4.5	2.46	0.16	29	0.40	0.04	0.02	0.09	7.7	7.1	0.6	8.3	4.5	6.4	27	8	65
FWP13-15*																	
0-20	4.4	3.90	0.38	80	0.43	0.13	1.80	1.51	4.6	3.5	1.1	8.3	0.9	72.8	12	5	83
20-48	4.7	3.50	0.25	58	0.36	0.09	1.21	1.36	5.1	3.9	1.2	8.0	1.1	65.5	18	5	76
48-82	4.9	3.50	0.27	25	0.39	0.01	0.53	0.87	6.8	5.3	1.5	8.6	1.6	46.6	24	5	71
82-119	4.9	3.30	0.21	20	0.35	0.01	0.46	1.23	10.6	8.4	2.2	12.6	2.7	40.1	41	6	53

* From Thompson *et al.* (1992a), Al^{3+}, total acidity and CEC values have been corrected.

Table 4.2. Soil chemical properties (n= 11 samples per plot) and particle size composition (n= 3 per plot) from surface soil (0-10 cm deep) from three plots in each forest type on Maracá Island. PRF= *Peltogyne*-rich forest (a) trail 1, (b) Maracá House, PPF= *Peltogyne*-poor forest, FWP= forest without *Peltogyne* (a) trail 1 (b) plots described by Thompson *et al.* (1992). n.a.= data not available. Values within a row followed by different letters are significantly different, others non-significant (two-way nested Anova, $p \leq 0.05$, multiple comparisons by Tukey test).

	PRFa	PRFb	PPF	FWPa	FWPb
Loss on ignition(%)	2.34^{a}	4.25^{b}	1.85^{a}	0.83^{a}	1.02^{a}
pH_{H2o}	4.6^{a}	4.3^{a}	4.4^{a}	4.4^{a}	4.9^{a}
N_{ext} ($\mu g\ g^{-1}$)	2.01^{a}	n.a.	2.09^{a}	1.13^{a}	n.a.
P_{ext} ($\mu g\ g^{-1}$)	2.15^{a}	n.a.	2.00^{a}	0.80^{b}	5.09^{c}
Exchangeable cations (mequiv.kg^{-1})					
K^{+}	1.09^{a}	1.06^{a}	1.00^{a}	0.45^{b}	0.66^{a}
Na^{+}	0.05^{a}	0.15^{b}	0.04^{a}	0.03^{a}	0.05^{a}
Ca^{2+}	$1.35^{a,d}$	$1.85^{a,d}$	$0.95^{a,b}$	0.46^{b}	$2.33^{c,d}$
Mg^{2+}	$3.43^{a,b}$	4.72^{a}	1.88^{b}	0.56^{c}	1.77^{b}
H^{+}	2.00^{a}	3.80^{a}	2.70^{a}	1.30^{a}	3.59^{a}
Al^{+}	4.30^{a}	14.4^{b}	3.10^{a}	2.00^{a}	$7.00^{a,b}$
CEC	$12.2^{a,b}$	26.0^{c}	$9.72^{a,b}$	4.84^{a}	16.3^{b}
Base saturation (%)	50.0	31.1	40.2	31.2	31.3
Mg^{2+}/Ca^{2+}	2.58^{a}	2.53^{a}	$1.98^{a,b}$	1.24^{c}	0.80^{c}
Mg^{2+}/total base	0.58^{a}	0.59^{a}	$0.48^{a,b}$	0.38^{c}	0.37^{c}
Clay (%)	16^{a}	35^{b}	16^{a}	12^{a}	12^{a}
Silt (%)	6^{a}	21^{b}	6^{a}	3^{c}	4^{c}
Sand (%)	78^{a}	45^{b}	78^{a}	86^{c}	86^{c}

sand and more silt than FWP (Table 4.2), and varied from loamy sandy (78% sand) to silt clay (45% sand) (Table 4.1 and Appendix 1). The values of loss-on-ignition were higher in PRF although the difference was only statistically significant between the PRFb plots and the other forest types. A fairly high base saturation (40% to 55%) was found for almost all soils, with the exception of those soils from plots PRFb and FWPa which both had 31%. The percentage of base saturations are ranked in the order PRFa>PPF>FWPb>FWPa≥PRFb.

FOREST STRUCTURE

Canopy height

Profile diagrams for each forest type are shown in Figures 4.3, 4.4 and 4.5. The PRF had the highest canopy (25-35 m), while the lowest value was found for PPF (20-26 m). All forest types had emergent trees reaching over 40 m tall with PRF having the most emergents and the tallest trees. It also had a better developed understorey (10-20 m tall). The PPF had a less well-developed understorey while the FWP had an open canopy and a poorly developed understorey.

Basal area and density

The structural data for each plot for trees ≥ 10 cm dbh are summarised in Table 4.3 and for trees ≥ 30 cm dbh in Table 4.4. PRF plots showed the highest and FWP plots the lowest values of basal area, number of individuals and maximum diameter.

The mean basal areas per hectare for each forest type in three different dbh classes are given in Table 4.5. PRF and PPF always had higher basal area values than FWP. However in the majority of the cases the values did not

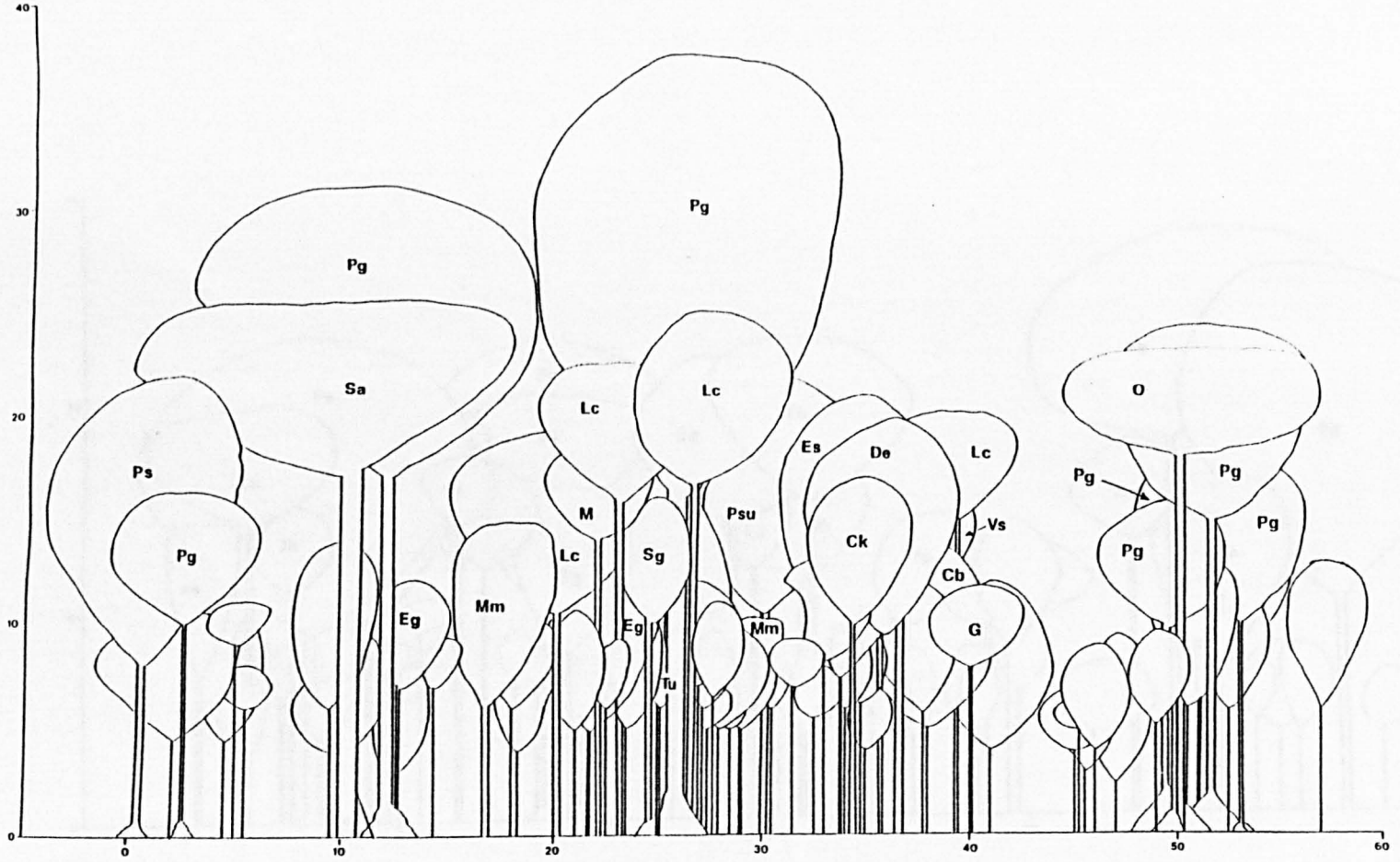


Figure 4.3. Profile diagram (60 m x 7.5 m) of forest at plot PRF2 on Maracá Island, Brazil. Trees less than 6 m high excluded. Symbols for trees over 10 cm dbh: Cb, *Chomelia barbellata*; Ck, *Chaunochiton kappleri*; De, *Duroia eriopila*; Eg, *Ecclinusa guianensis*; Es, *Enterolobium schomburgkii*; G, *Guapira* sp.; Lc, *Lecythis corrugata*; M, *Machaerium* sp.; Mm, *Maximiliana maripa*, O, *Ormosia smithii*; Pg, *Peltogyne gracilipes*; Ps, *Pradosia surinamensis*; Psu, *Pouteria surumuensis*; Sa, *Simarouba amara*; Sg, *Swartzia grandifolia*; Tu, *Tabebuia uleana*; Vs, *Vitex schomburgkiana*.

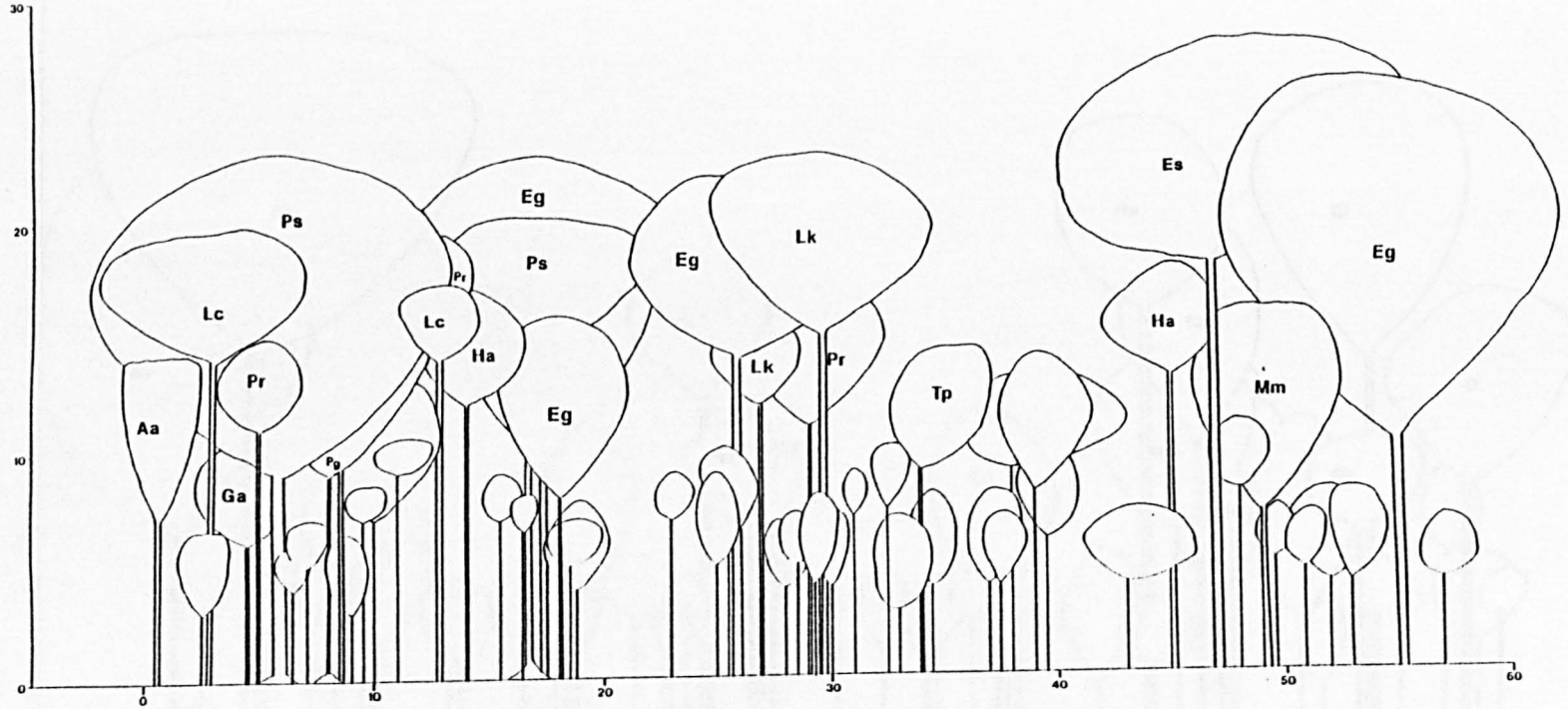


Figure 4.4. Profile diagram (60 m x 7.5 m) of forest at plot PPF9 on Maracá Island, Brazil. Trees less than 6 m high excluded. Symbols for trees over 10 cm dbh: Aa, *Astrocaryum aculeatum*; Eg, *Ecclinusa guianensis*; Es, *Enterolobium schomburgkii*; Ga, *Gustavia augusta*; Ha, *Himatanthus articulatus*; Lc, *Lecythis corrugata*; Lk, *Licania kunthiana*; Mm, *Maximiliana maripa*; Pg, *Peltogyne gracilipes*; Pr, *Pouteria reticulata*; Ps, *Pradosia surinamensis*; Tp, *Tetragastris panamensis*.

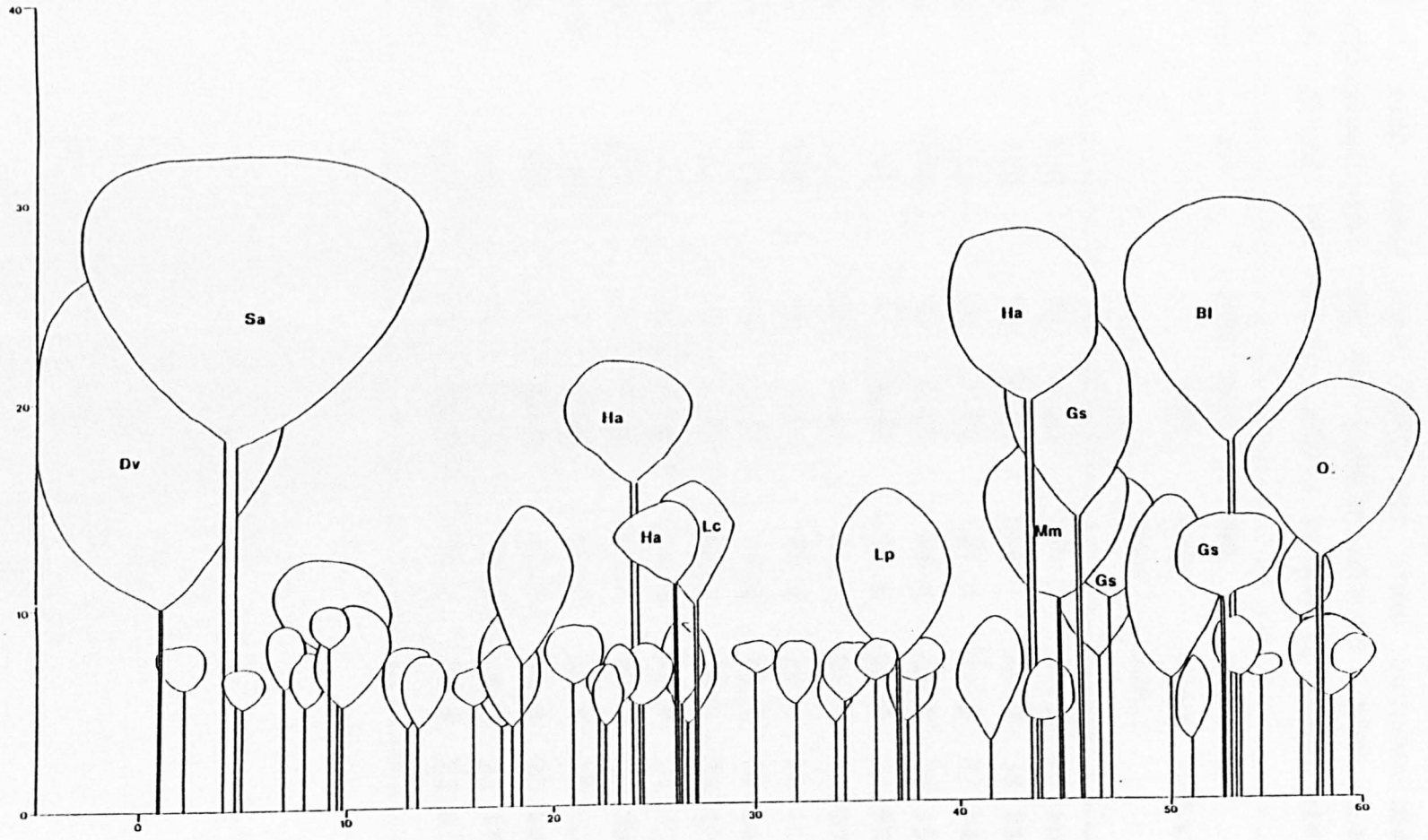


Figure 4.5. Profile diagram (60 m x 7.5 m) of forest at plot FWP10 on Maracá Island, Brazil. Trees less than 6 m high excluded. Symbols for trees over 10 cm dbh: Bl, *Brosimum lactescens*, Dv, *Drypetes variabilis*; Gs, *Guatteria schomburgkiana*; Ha, *Himatanthus articulatus*; Lc, *Lecythis corrugata*; Lp, *Lindackeria paludosa*; Mm, *Maximiliana maripa*; O, *Ormosia smithii*; Sa, *Simarouba amara*.

Table 4.3. Trees (≥ 10 dbh) density (N), number of species (Spp.), mean basal area (MBA) per tree, maximum dbh, mean dbh and basal area (BA) for each 50 m x 50 m plot studied on Maracá Island, RR, Brazil. Plots ranked by basal area.

Plots	N	Spp.	MBA (m^2)	dbh max. (cm)	dbh mean (cm)	BA (m^2ha^{-1})
PRF5	110	27	0.10	143.2	26.1	43.10
PRF2	129	29	0.07	134.3	23.9	38.33
PRF4	150	19	0.06	127.3	22.2	37.54
PRF6	175	18	0.05	64.6	22.8	36.75
PPF8	95	31	0.09	132.6	28.4	34.90
PRF3	137	24	0.06	83.7	24.2	34.77
PPF9	132	24	0.06	92.6	24.3	34.11
PPF7	115	40	0.07	79.6	24.4	30.41
FWP11	101	33	0.07	86.1	25.1	28.12
FWP12	102	28	0.07	60.6	25.9	27.90
FWP15	117	45	0.06	105.7	22.2	26.94
FWP10	106	33	0.06	60.2	24.4	25.62
PRF1	118	26	0.05	77.5	22.4	25.24
FWP14	107	41	0.05	83.3	21.8	22.96
FWP13	117	41	0.05	72.8	21.6	22.01

Table 4.4. Tree (≥ 30 cm dbh) density (N), number of species (Spp.), mean basal area (MBA) per tree, maximum dbh, mean dbh and basal area for each 50 m x 50 m plot studied on Maracá Island, RR, Brazil. Plots ranked by basal area.

Plots	N	Spp.	MBA (m^2)	dbh max. (cm)	dbh mean (cm)	BA (m^2ha^{-1})
PRF5	29	11	0.32	143.2	57.6	36.88
PRF2	27	7	0.27	134.3	53.2	28.95
PPF8	33	12	0.21	132.6	46.5	27.46
PRF4	20	4	0.31	127.3	57.4	24.81
PPF9	35	11	0.18	92.6	45.3	24.71
PRF3	33	8	0.18	83.7	46.6	24.20
PRF6	39	5	0.15	64.6	42.5	23.15
PPF7	33	15	0.17	79.6	44.6	22.76
FWP12	36	11	0.15	60.6	42.8	21.39
FWP11	26	10	0.19	86.1	47.8	20.30
FWP15	19	13	0.23	105.7	50.3	17.46
FWP10	26	7	0.16	60.2	44.0	16.36
PRF1	25	10	0.15	77.5	42.0	15.41
FWP14	19	5	0.19	83.3	47.1	14.75
FWP13	25	11	0.13	72.8	40.2	13.39

Table 4.5. Mean (and ranges) of basal areas ha^{-1} of trees in three size classes in three replicate 50 m X 50 m plots in three evergreen forest types on Maracá Island, RR, Brazil. Values within a row followed by different letters are significantly different, others non-significant (one-way Anova, $p \leq 0.05$, multiple comparisons by Tukey test).

Dbh class	Forest types				
	PRFa	PRFb	PPF	FWPa	FWPb
≥ 10 cm	32.8[a] (25.2-38.3)	39.1[b] (36.7-43.1)	33.1[a] (30.4-34.9)	27.1[a] (25.6-28.1)	24.0[a] (22.0-26.9)
≥ 30 cm	22.8[a] (15.3-28.9)	28.3[a] (23.2-37.0)	24.9[a] (22.6-27.4)	19.3[a] (16.4-21.4)	15.2[a] (13.4-17.4)
≥ 50 cm	13.1[a] (6.3-21.8)	19.1[a] (8.9-29.2)	13.3[a] (11.2-16.4)	7.8[a] (5.8-10.9)	8.4[a] (3.3-12.1)

PRF- *Peltogyne*-rich forest, PPF- *Peltogyne*-poor forest, FWP- forest without *Peltogyne*.

Table 4.6. Mean stem density in three replicate 50 m x 50 m plots in three evergreen forest types on Maracá Island, Brazil. PRF- *Peltogyne*-rich forest, PPF- *Peltogyne*-poor forest, FWP- forest without *Peltogyne*. Seedlings, ≤ 50 cm tall; saplings > 50 cm tall and < 10 cm dbh; small trees ≥ 10 cm dbh; trees, ≥ 30 cm dbh and large trees, ≥ 50 cm dbh.

Size class	plot size (m^2)	no. of sub-plots	mean stems demsity				
			PRFa	PRFb	PPF	FWPa	FWPb
Seedlings (m^{-2})	2	5	23.23	8.13	10.73	8.33	6.22
Saplings (m^{-2})	16	5	3.31	2.91	2.34	1.58	2.92
Small trees (ha^{-1})	100	25	401	463	321	295	379
Trees (ha^{-1})	100	25	83	75	101	89	59
Large trees (ha^{-1})	100	25	31	43	33	28	23

differ statistically.

The diameter distribution patterns of plants were similar among forests and each plot showed a reversed-J shape curve. All plots had a high density of stems 10-30 cm in dbh and a paucity of trees more than 50 cm dbh (Fig. 4.6), with the largest trees occurring most often in PRF. No difference among forests was found for the number of individuals, but PRF tended to have more small trees (≥10 cm - ≤ 30 cm dbh) than the other forests (Table 4.6). Seedling and sapling abundance were also higher in PRF (Table 4.6). In both sites (PRFa and PRFb), *Peltogyne* seedlings accounted for about 60% of all seedlings, while its saplings accounted for 40% of all saplings (see Chapter 6 for details). Table 4.7 shows the abundance of small palms and large-leaved herbs on the floor of each forest type. The lowest densities of these plants were found in PRF. The number of standing and fallen dead trees ≥ 10 cm dbh was similar among forest types, with a tendency for more dead trees in PPF, but when only large dead trees (≥ 50 cm dbh) were considered PRF had higher values than FWP (Table 4.8).

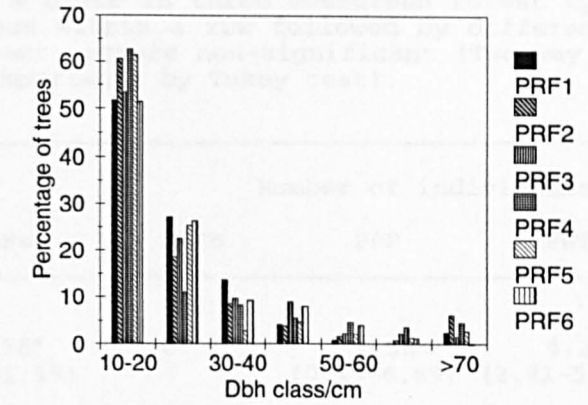
Lianas and forest type

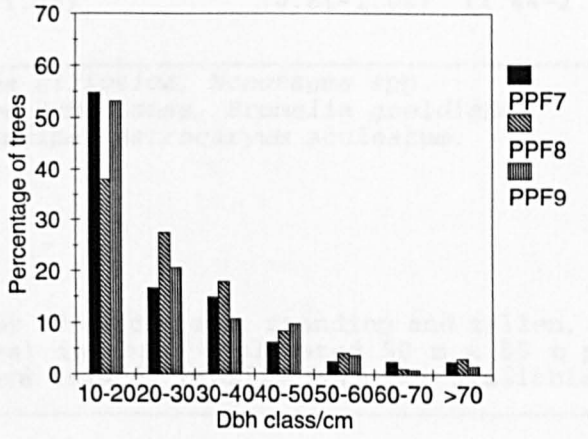
PRFa had more trees supporting one or more lianas than the other forest types (Table 4.9) and about 50% of the *Peltogyne* trees supported lianas in PRFa, while in PPF only 15% of them had lianas.

FLORISTICS

Level of identification

About 90% of the individuals (n= 1666) have been identified to species with 110 trees identified to genus and 35 trees not determined at all. However, the latter have





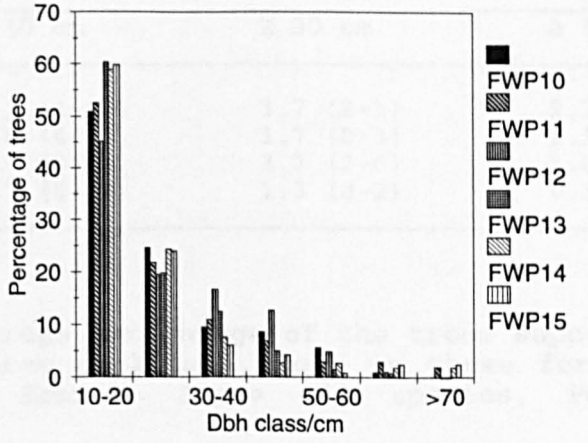


Figure 4.6. Distribution of diameters of trees (>= 10 cm) in each study plot in PRF, PPF, and FWP.

Table 4.7. Means (and ranges) of density (m^{-2}) of small palms and large-leaved herbs (Marantaceae and Bromeliaceae) on the floor of three replicate 50 m x 50 m plots in three evergreen forest types on Maracá island, Brazil. Values within a row followed by different letters are significantly different, others non-significant (Two-way nested Anova, $p \leq 0.05$, multiple comparisons by Tukey test).

	Number of individuals (m^{-2})				
	PRFa	PRFb	PPF	FWPa	FWPb
Marantaceae + Bromeliaceae	0.56^{a} (0-1.19)	0^{b}	2.56^{c} (0.19-6.69)	4.21^{c} (2.81-5.87)	2.18^{c} (0.1-4.1)
Small palm	0.87^{a} (0.44-1.25)	0^{b}	0.96^{a} (0.81-1.06)	1.98^{c} (1.44-2.81)	0.43^{a} (0.3-0.6)

Marantaceae- *Calathea elliptica, Monotagma* spp.
Bromeliaceae- *Aechmea rubiginosa, Bromelia goeldiana.*
palms- *Maximiliana maripa, Astrocaryum aculeatum.*

Table 4.8. Mean number of dead trees, standing and fallen, per size class (range in parentheses) in three replicated 50 m x 50 m plots in three forest types on Maracá Island, Brazil. Data not available for FWPb.

Forest	Size class (dbh)		
	≥ 10 cm	≥ 30 cm	≥ 50 cm
PRFa	7.3 (4-12)	3.7 (2-5)	2.7 (2-3)
PRFb	7.0 (4-11)	1.7 (0-3)	1.3 (0-3)
PPF	9.7 (9-10)	3.7 (2-6)	1.0 (1-1)
FWPa	6.7 (5- 8)	1.3 (0-2)	0.3 (0-1)

Table 4.9. The average percentage of the trees supporting one or more lianas in three replicate plots in three forest types on Maracá, Roraima, Brazil. Spp.= all species, PG= *Peltogyne gracilipes*.

Plot	PRFa		PPF		FWPa
	Spp.	PG	Spp.	PG	Spp.
1	59	67	44	29	19
2	35	36	42	17	22
3	26	38	17	0	26
Mean	40	47	34	15	22

been assigned to 16 taxa, representing 1.8% of the trees.

Family composition

The list of families of trees ≥ 10 cm, ≥ 30 cm, and ≥ 50 cm dbh and their number of individuals, number of species, mean basal area and cover value indices for each forest type are shown in tables 4.10-4.16.

Density contribution

In terms of densities of trees (≥10 cm dbh), the Sapotaceae were the most abundant family in all forest types and only this family and the Rubiaceae occurred among the ten most abundant families in all forest types. Families such as the Apocynaceae, Chysobalanaceae, Lecythidaceae and Palmae, were among the most abundant families in most of the forests, except in PRFb (Table 4.10). The Fabaceae were abundant only in PRF, while the Annonaceae, Burseraceae and Moraceae were very abundant in FWP (Tables 4.10 and 4.12).

For trees (≥ 30 cm dbh) (Tables 4.13-4.15), the most abundant family in PRF were the Caesalpiniaceae, with on average 25% of the trees, followed by the Sapotaceae (19%, PRFa) and the Mimosaceae (16%, PRFb) (Table 4.13). In PPF, the Sapotaceae were the most abundant family, with 38% of the individuals, followed by the Chysobalanaceae (12%) and Caesalpiniaceae (11%) (Table 4.14). The Sapotaceae and Chrysobalanaceae were also the most abundant families in the FWPa plots with on average 38% and 21% of the individuals, respectively (Table 4.15). In FWPb, the Moraceae and Sapotaceae were the most abundant family with 22% of the trees, but the former family occurred with only 3% of the trees in FWPa.

When only larger trees (≥50 cm dbh) were considered (Table 4.16), the Caesalpiniaceae occurred with up to 91% of

Table 4.10. Families of trees ≥ 10 cm dbh occurring in three replicate 50 m x 50 m plots in each of two PRF's, (a) at trail 1 and (b) at Maracá House on Maracá Island, RR, Brazil with number of individuals (N), number of species (Spp.), percentage of species (%Spp.), basal area (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI). Families ranked by CVI.

Family	N	Spp.	%Spp.	BA (m^2)	RD (%)	RDo (%)	CVI (%)
PRFa							
Caesalpiniaceae	84	2	4.26	13.10	21.88	53.30	75.17
Sapotaceae	95	6	12.77	3.82	24.74	15.55	40.29
Palmae	29	2	4.26	1.64	7.55	6.63	14.19
Lecythidaceae	31	1	2.13	1.06	8.07	4.30	12.38
Bignoniaceae	28	1	2.13	0.92	7.29	3.73	11.02
Simaroubaceae	24	2	4.26	1.12	6.25	4.57	10.82
Rubiaceae	32	5	10.64	0.55	8.33	2.25	10.58
Fabaceae	12	5	10.64	0.34	3.13	1.38	4.51
Chrysobalanaceae	8	3	6.38	0.46	2.08	1.88	3.96
Apocynaceae	8	2	4.26	0.19	2.08	0.77	2.85
Mimosaceae	4	1	2.13	0.44	1.04	1.80	2.84
Olacaceae	4	1	2.13	0.30	1.04	1.21	2.25
Myrtaceae	5	2	4.26	0.10	1.30	0.42	1.72
Unidentified	5	3	6.38	0.08	1.30	0.33	1.63
Tiliaceae	4	2	4.26	0.11	1.04	0.47	1.51
Verbenaceae	2	1	2.13	0.13	0.52	0.53	1.06
Euphorbiaceae	2	1	2.13	0.05	0.52	0.20	0.72
Annonaceae	1	1	2.13	0.05	0.26	0.20	0.47
Combretaceae	1	1	2.13	0.04	0.26	0.16	0.42
Burseraceae	1	1	2.13	0.02	0.26	0.10	0.36
Menispermaceae	1	1	2.13	0.02	0.26	0.07	0.33
Malpighiaceae	1	1	2.13	0.02	0.26	0.06	0.32
Moraceae	1	1	2.13	0.01	0.26	0.05	0.31
Nyctaginaceae	1	1	2.13	0.01	0.26	0.03	0.30
PRFb							
Caesalpiniaceae	128	5	11.90	18.57	29.43	63.28	92.70
Mimosaceae	64	2	4.76	3.13	14.71	10.67	25.38
Sapotaceae	64	3	7.14	2.69	14.71	9.17	23.88
Myrtaceae	44	1	2.38	0.70	10.11	2.37	12.49
Rubiaceae	29	5	11.90	0.62	6.67	2.11	8.77
Boraginaceae	24	1	2.38	0.82	5.52	2.79	8.31
Unidentified	16	6	14.29	0.50	3.68	1.72	5.40
Flacourtiaceae	19	1	2.38	0.22	4.37	0.74	5.11
Tiliaceae	7	1	2.38	0.45	1.61	1.52	3.13
Fabaceae	4	4	9.52	0.55	0.92	1.89	2.81
Violaceae	9	1	2.38	0.16	2.07	0.54	2.61
Bignoniaceae	5	1	2.38	0.35	1.15	1.18	2.33
Simaroubaceae	4	1	2.38	0.05	0.92	0.18	1.10
Lauraceae	4	1	2.38	0.05	0.92	0.16	1.08
Apocynaceae	2	1	2.38	0.13	0.46	0.44	0.90
Moraceae	1	1	2.38	0.18	0.23	0.62	0.85
Chrysobalanaceae	3	1	2.38	0.04	0.69	0.13	0.82
Combretaceae	2	1	2.38	0.04	0.46	0.13	0.59
Erythroxylaceae	2	1	2.38	0.02	0.46	0.08	0.54
Opiliaceae	1	1	2.38	0.05	0.23	0.16	0.39
Annonaceae	1	1	2.38	0.02	0.23	0.05	0.28
Rutaceae	1	1	2.38	0.01	0.23	0.05	0.28
Quiinaceae	1	1	2.38	0.01	0.23	0.03	0.26

Table 4.11. Families of trees ≥ 10 cm dbh occurring in three replicate 50 m x 50 m plots in PPF at trail 1 on Maracá Island, RR, Brazil with number of individuals (N), number of species (Spp.), percentage of species (%Spp.), basal area (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI). Families ranked by CVI.

Family	N	Spp.	%Spp.	BA (m^2)	RD (%)	RDo (%)	CVI (%)
PPF							
Sapotaceae	91	8	14.55	7.63	26.61	30.71	57.32
Caesalpiniaceae	16	1	1.82	4.98	4.68	20.05	24.73
Lecythidaceae	43	4	7.27	2.38	12.57	9.56	22.14
Burseraceae	39	2	3.64	1.52	11.40	6.12	17.52
Chrysobalanaceae	27	4	7.27	2.37	7.89	9.52	17.42
Palmae	30	3	5.45	1.65	8.77	6.66	15.43
Simaroubaceae	15	2	3.64	1.58	4.39	6.34	10.20
Rubiaceae	17	4	7.27	0.41	4.97	1.63	6.61
Moraceae	11	1	1.82	0.74	3.22	2.97	6.19
Apocynaceae	9	2	3.64	0.59	2.63	2.36	4.99
Annonaceae	7	2	3.64	0.18	2.05	0.74	2.79
Euphorbiaceae	5	1	1.82	0.19	1.46	0.78	2.25
Mimosaceae	3	2	3.64	0.21	0.88	0.86	1.74
Flacourtiaceae	4	2	3.64	0.09	1.17	0.36	1.53
Ulmaceae	4	1	1.82	0.09	1.17	0.36	1.52
Tiliaceae	4	2	3.64	0.06	1.17	0.25	1.42
Lauraceae	3	2	3.64	0.08	0.88	0.32	1.20
Unidentified	3	3	5.45	0.06	0.88	0.24	1.12
Fabaceae	3	2	3.64	0.05	0.88	0.21	1.08
Myrtaceae	2	1	1.82	0.04	0.58	0.16	0.74
Meliaceae	1	1	1.82	0.02	0.29	0.09	0.38
Menispermaceae	1	1	1.82	0.02	0.29	0.06	0.36
Ochnaceae	1	1	1.82	0.01	0.29	0.05	0.34
Malpighiaceae	1	1	1.82	0.01	0.29	0.04	0.33
Bignoniaceae	1	1	1.82	0.01	0.29	0.04	0.33
Hippocrateaceae	1	1	1.82	0.01	0.29	0.03	0.32

Table 4.12. Families of trees ≥ 10 cm dbh occurring in three replicate 50 m x 50 m plots in two FWP sites (a) at trail 1 and (b) in Thompson's *et al.* (1992a) plots on Maracá Island, RR, Brazil with number of trees (N), number of species (Spp.), percentage of species (%Spp.), basal area (BA), relative density (RD), relative dominance (RDo), cover value index (CVI). Families ranked by CVI.

Family	N	Spp.	%Spp.	BA (m^2)	RD (%)	RDo (%)	CVI (%)
FWPa							
Sapotaceae	81	6	11.76	7.49	26.21	36.72	62.93
Chrysobalanaceae	37	2	3.92	4.17	11.97	20.42	32.39
Palmae	28	3	5.88	1.52	9.06	7.43	16.49
Lecythidaceae	22	2	3.92	1.44	7.12	7.05	14.17
Burseraceae	20	2	3.92	1.32	6.47	6.49	12.96
Annonaceae	25	3	5.88	0.70	8.09	3.44	11.53
Apocynaceae	20	2	3.92	0.87	6.47	4.28	10.75
Simaroubaceae	5	1	1.96	0.95	1.62	4.64	6.26
Rubiaceae	16	4	7.84	0.21	5.18	1.04	6.22
Moraceae	7	1	1.96	0.55	2.27	2.69	4.96
Lauraceae	8	2	3.92	0.48	2.59	2.37	4.96
Euphorbiaceae	8	2	3.92	0.25	2.59	1.25	3.84
Flacourtiaceae	6	2	3.92	0.09	1.94	0.42	2.37
Fabaceae	4	3	5.88	0.06	1.29	0.28	1.57
Ulmaceae	3	1	1.96	0.05	0.97	0.24	1.21
Unidentified	3	2	3.92	0.05	0.97	0.22	1.19
Ochnaceae	3	1	1.96	0.03	0.97	0.17	1.14
Mimosaceae	3	2	3.92	0.03	0.97	0.17	1.14
Tiliaceae	2	2	3.92	0.03	0.65	0.17	0.82
Elaeocarpaceae	2	2	3.92	0.02	0.65	0.11	0.75
Bignoniaceae	1	1	1.96	0.04	0.32	0.18	0.50
Celastraceae	1	1	1.96	0.01	0.32	0.06	0.38
Opiliaceae	1	1	1.96	0.01	0.32	0.05	0.37
Myrtaceae	1	1	1.96	0.01	0.32	0.04	0.37
Caesalpiniaceae	1	1	1.96	0.01	0.32	0.04	0.36
Quiinaceae	1	1	1.96	0.01	0.32	0.04	0.36
FWPb							
Sapotaceae	52	8	11.43	2.81	15.25	15.65	30.90
Moraceae	28	4	5.71	3.64	8.21	20.26	28.47
Chrysobalanaceae	22	1	1.43	3.35	6.45	18.63	25.08
Burseraceae	28	3	4.29	1.79	8.21	9.96	18.17
Annonaceae	40	5	7.14	0.81	11.73	4.50	16.23
Rubiaceae	28	8	11.43	0.92	8.21	5.10	13.31
Palmae	26	2	2.86	0.95	7.62	5.28	12.91
Lecythidaceae	15	1	1.43	0.76	4.40	4.21	8.60
Apocynaceae	16	2	2.86	0.32	4.69	1.79	6.49
Flacourtiaceae	14	3	4.29	0.15	4.11	0.84	4.94
Unidentified	6	5	7.14	0.39	1.76	2.16	3.92
Dilleniaceae	8	1	1.43	0.23	2.35	1.30	3.65
Fabaceae	5	5	7.14	0.36	1.47	1.98	3.45
Lauraceae	7	3	4.29	0.17	2.05	0.93	2.98
Tiliaceae	7	2	2.86	0.16	2.05	0.89	2.95
Myrtaceae	6	2	2.86	0.15	1.76	0.85	2.61
Boraginaceae	5	1	1.43	0.20	1.47	1.12	2.59
Simaroubaceae	4	1	1.43	0.22	1.17	1.25	2.42
Elaeocarpaceae	6	1	1.43	0.11	1.76	0.61	2.37
Araliaceae	3	1	1.43	0.12	0.88	0.65	1.53
Ochnaceae	3	1	1.43	0.05	0.88	0.28	1.16
Ulmaceae	2	1	1.43	0.05	0.59	0.27	0.85
Mimosaceae	2	1	1.43	0.03	0.59	0.18	0.76
Caesalpiniaceae	1	1	1.43	0.08	0.29	0.42	0.71
Meliaceae	1	1	1.43	0.06	0.29	0.34	0.63
Anacardiaceae	1	1	1.43	0.04	0.29	0.22	0.51
Hippocrateaceae	1	1	1.43	0.02	0.29	0.11	0.40
Sapindaceae	1	1	1.43	0.01	0.29	0.08	0.37
Myristicaceae	1	1	1.43	0.01	0.29	0.07	0.36
Bignoniaceae	1	1	1.43	0.01	0.29	0.06	0.35
Combretaceae	1	1	1.43	0.01	0.29	0.05	0.34

Table 4.13. Families of trees ≥ 30 cm dbh occurring in three replicate 50 m x 50 m plots in two PRF sites, (a) at trail 1 and (b) at Maracá House on Maracá Island, RR, Brazil with, number of individuals (N), number of species (Spp.), percentage of species (%Spp.), basal area (m^2), relative density (RD), relative dominance (RDo) and cover value index (CVI). Families ranked by CVI.

Family	N	Spp.	%Spp.	BA (m^2)	RD (%)	RDo (%)	CVI (%)
PRFa							
Caesalpiniaceae	46	1	6.67	12.35	54.12	72.06	126.17
Sapotaceae	16	2	13.33	1.86	18.82	10.83	29.66
Simaroubaceae	3	1	6.67	0.86	3.53	4.99	8.52
Lecythidaceae	4	1	6.67	0.36	4.71	2.08	6.79
Palmae	4	1	6.67	0.30	4.71	1.78	6.49
Mimosaceae	3	1	6.67	0.37	3.53	2.18	5.71
Chrysobalanaceae	2	2	13.33	0.33	2.35	1.95	4.30
Olacaceae	2	1	6.67	0.27	2.35	1.58	3.93
Verbenaceae	1	1	6.67	0.12	1.18	0.69	1.87
Bignoniaceae	1	1	6.67	0.10	1.18	0.57	1.75
Rubiaceae	1	1	6.67	0.08	1.18	0.45	1.63
Fabaceae	1	1	6.67	0.07	1.18	0.42	1.60
Apocynaceae	1	1	6.67	0.07	1.18	0.41	1.59
PRFb							
Caesalpiniaceae	55	1	6.67	16.48	62.50	77.69	140.19
Mimosaceae	14	2	13.33	1.87	15.91	8.81	24.72
Sapotaceae	8	3	20.00	1.10	9.09	5.20	14.29
Fabaceae	2	2	13.33	0.52	2.27	2.45	4.73
Bignoniaceae	2	1	6.67	0.29	2.27	1.36	3.63
Tiliaceae	2	1	6.67	0.20	2.27	0.97	3.24
Moraceae	1	1	6.67	0.18	1.14	0.86	2.00
Unidentified	1	1	6.67	0.17	1.14	0.81	1.94
Boraginaceae	1	1	6.67	0.17	1.14	0.80	1.93
Rubiaceae	1	1	6.67	0.11	1.14	0.53	1.67
Apocynaceae	1	1	6.67	0.11	1.14	0.53	1.66

Table 4.14. Families of trees ≥ 30 cm dbh occurring in three replicate 50 m x 50 m plots in PPF sites at trail 1 on Maracá Island, RR, Brazil with number of individuals (N), number of species (Spp.), percentage of species (%Spp.), basal area (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI). Families ranked by CVI.

Family	N	Spp.	%Spp.	BA (m^2)	RD (%)	RDo (%)	CVI (%)
PPF							
Sapotaceae	38	6	31.58	6.20	37.62	33.10	70.72
Caesalpiniaceae	11	1	5.26	4.85	10.89	25.93	36.82
Chrysobalanaceae	12	1	5.26	1.92	11.88	10.29	22.17
Simaroubaceae	10	1	5.26	1.46	9.90	7.79	17.69
Lecythidaceae	8	2	10.53	1.49	7.92	7.97	15.89
Burseraceae	5	1	5.26	0.75	4.95	4.02	8.97
Palmae	6	1	5.26	0.47	5.94	2.50	8.44
Apocynaceae	4	2	10.53	0.48	3.96	2.55	6.51
Moraceae	3	1	5.26	0.60	2.97	3.21	6.18
Euphorbiaceae	2	1	5.26	0.17	1.98	0.89	2.87
Mimosaceae	1	1	5.26	0.17	0.99	0.91	1.90
Rubiaceae	1	1	5.26	0.16	0.99	0.86	1.85

Table 4.15. Families of trees ≥ 30 cm dbh occurring in three replicate 50 m x 50 m plots in two FWP sites at trail 1 on Maracá Island, RR, Brazil with number of individuals (N), number of species (Spp.), percentage of species (%Spp.), basal area (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI). Families ranked by CVI.

Family	N	Spp.	%Spp.	BA (m^2)	RD (%)	RDo (%)	CVI (%)
FWFa							
Sapotaceae	38	3	20.00	6.15	43.18	42.39	85.57
Chrysobalanaceae	19	1	6.67	3.42	21.59	23.57	45.17
Burseraceae	8	1	6.67	1.17	9.09	8.08	17.17
Lecythidaceae	4	2	13.33	1.03	4.55	7.07	11.61
Simaroubaceae	4	1	6.67	0.93	4.55	6.44	10.98
Palmae	6	1	6.67	0.47	6.82	3.27	10.09
Moraceae	3	1	6.67	0.45	3.41	3.12	6.53
Lauraceae	3	2	13.33	0.40	3.41	2.79	6.19
Apocynaceae	2	2	13.33	0.30	2.27	2.10	4.38
Annonaceae	1	1	6.67	0.17	1.14	1.17	2.31
FWPb							
Moraceae	14	3	15.00	3.08	22.22	27.00	49.22
Chrysobalanaceae	12	1	5.00	3.03	19.05	26.60	45.65
Sapotaceae	14	4	20.00	1.81	22.22	15.88	38.10
Burseraceae	9	1	5.00	1.53	14.29	13.41	27.69
Lecythidaceae	4	1	5.00	0.39	6.35	3.46	9.81
Fabaceae	2	2	10.00	0.25	3.17	2.18	5.35
Rubiaceae	1	1	5.00	0.42	1.59	3.65	5.24
Unidentified	1	1	5.00	0.33	1.59	2.91	4.50
Boraginaceae	1	1	5.00	0.11	1.59	1.01	2.60
Simaroubaceae	1	1	5.00	0.11	1.59	0.94	2.53
Dilleniaceae	1	1	5.00	0.10	1.59	0.86	2.45
Lauraceae	1	1	5.00	0.08	1.59	0.72	2.31
Araliaceae	1	1	5.00	0.08	1.59	0.71	2.30
Caesalpiniaceae	1	1	5.00	0.07	1.59	0.66	2.25

Table 4.16. Families of trees ≥ 50 cm dbh occurring in three replicate 50 m x 50 m plots in PRF, PPF and FWP sites at trail 1 (a) and at Maracá House (b) on Maracá Island, RR, Brazil with number of individuals (N), number of species (Spp.), percentage of species (%Spp.), basal area (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI). Families ranked by CVI.

Family	N	Spp.	%Spp.	BA (m^2)	RD (%)	RDo (%)	CVI (%)
PRFa							
Caesalpiniaceae	21	1	33.33	8.94	91.30	90.87	182.18
Simaroubaceae	1	1	33.33	0.64	4.35	6.47	10.82
Chrysobalanaceae	1	1	33.33	0.26	4.35	2.65	7.00
PRFb							
Caesalpiniaceae	26	1	20.00	12.73	81.25	89.07	170.32
Mimosaceae	2	1	20.00	0.56	6.25	3.91	10.16
Sapotaceae	2	1	20.00	0.47	6.25	3.29	9.54
Fabaceae	1	1	20.00	0.33	3.13	2.34	5.46
Bignoniaceae	1	1	20.00	0.20	3.13	1.40	4.52
PPF							
Caesalpiniaceae	7	1	11.11	4.23	28.00	42.41	70.41
Sapotaceae	9	3	33.33	3.01	36.00	30.19	66.19
Lecythidaceae	2	1	11.11	0.90	8.00	9.04	17.04
Chrysobalanaceae	2	1	11.11	0.54	8.00	5.42	13.42
Burseraceae	2	1	11.11	0.45	8.00	4.52	12.52
Simaroubaceae	2	1	11.11	0.43	8.00	4.36	12.36
Moraceae	1	1	11.11	0.40	4.00	4.07	8.07
FWPa							
Sapotaceae	8	2	25.00	2.27	38.10	38.76	76.86
Chrysobalanaceae	6	1	12.50	1.51	28.57	25.70	54.27
Simaroubaceae	3	1	12.50	0.81	14.29	13.75	28.03
Lecythidaceae	2	2	25.00	0.81	9.52	13.87	23.39
Moraceae	1	1	12.50	0.24	4.76	4.17	8.93
Burseraceae	1	1	12.50	0.22	4.76	3.75	8.51
FWPb							
Chrysobalanaceae	6	1	12.50	2.27	35.29	36.00	71.29
Moraceae	4	3	37.50	2.04	23.53	32.45	55.97
Burseraceae	4	1	12.50	1.04	23.53	16.51	40.04
Rubiaceae	1	1	12.50	0.42	5.88	6.62	12.50
Unidentified	1	1	12.50	0.33	5.88	5.27	11.15
Sapotaceae	1	1	12.50	0.20	5.88	3.15	9.03

the trees in PRF. For the PPF and FWPa the Sapotaceae were the most important family with about 36% of the trees followed by the Caesalpiniaceae (28%, in PPF) and Chrysobalanaceae (29%, in FWPa). For the FWPb the Chrysobalanaceae were the most abundant family (35% of the trees) followed by the Moraceae and Burseraceae both with 24% of the trees.

Basal area contribution

The family abundance in terms of basal area of trees ≥ 10 cm, ≥ 30 cm and ≥ 50 cm dbh showed the same patterns observed for density (Tables 4.10-4.16). The Caesalpiniaceae had the highest basal area in PRF contributing up to 63% of the trees (≥ 10 cm dbh), while the Sapotaceae had the highest basal area in FWP (up to 36% of the trees). As found for density, the Sapotaceae were among the families with the highest basal area in all forest types. The Chrysobalanaceae abundance ranking was PRF>PPF>FWP, with the opposite occurring for Caesalpiniaceae.

For trees (≥ 30 cm), the percentage of basal area of the Caesalpiniaceae in PRF was on average 75% followed by Sapotaceae with 10%, showing a high dominance by the former in this forest type (Table 4.13). In PPF, the Caesalpiniaceae were also important (26%), but the Sapotaceae had higher dominance values (33%) (Table 4.14). The Sapotaceae, Moraceae and Chrysobalanaceae were the most dominant families in FWP, with these families contributing on average 69% of the total basal area (Table 4.15). With increasing minimum dbh to 50 cm the dominance value for the Caesalpiniaceae increased to on average 90% in PRF and to 42% in PPF. For the FWP, the Chrysobalanaceae had on the average the highest dominance values (31%), followed by the Sapotaceae (21%) and Moraceae (18%) (Table 4.16).

Species contribution

The Sapotaceae and Rubiaceae occurred with the highest number of species for trees (≥ 10 cm dbh) in all the forest types, representing about 12% and 10% of the total number (Tables 4.10-4.12). The Sapotaceae had also the highest percentage of species for larger trees (≥ 30 cm and ≥ 50 cm dbh) (Tables 4.13-4.16). The Rubiaceae showed notably low values of numbers of species for the large dbh classes.

The number of species per family was not related to the abundance or the basal area of a family. The Rubiaceae always occupied fifth place or more when the families were ranked by the cover value index. The Caesalpiniaceae, the most dominant family (53%) in PRFa, occurred with only two species, while the Sapotaceae with six species had only 16% of the dominance. The Chrysobalanaceae had four species in PPF and only 9.5% of the total basal area, while in FWPb this family occurred with one species and contributed 19% of the total basal area.

Similarity and diversity among forests

The family similarities among forest types were very high with Sørensen's coefficient values (CCs) between the plots always higher than 64%. However, *Peltogyne*-rich forests had the lowest values for the number of families and family diversity indices (Table 4.17).

Structural classification

A classification, following Newbery *et al.* (1992), of the families into three different categories (overstorey, intermediate and understorey) was done for the 10 most important families in each forest type based on the relation between the ratio of basal area and density for trees ≥ 30

Table 4.17. Family diversity and similarity amongst the three forest types studied on Maracá Island, RR, Brazil. S= number of families.

Family diversity
(Shannon Index)

	PRFa	PRFb	PPF	FWPa	FWPb
H'	2.35	2.31	2.54	2.56	2.86
S	24	23	26	26	31

Family similarity
(Sørensen Index)

PRFa x PRFb	PRFa x PPF	PRFa x FWPa	PRFa x FWPb
64%	80%	72%	69%
PRFb x PPF	PRFb x FWPa	PRFb x FWPb	PPF x FWPa
69%	73%	67%	85%
PPF x FWPb	FWPa x FWPb		
84%	77%		

cm dbh to that for trees ≥ 10 cm dbh and the results are shown in Figures 4.7 and 4.8. Families with a basal area ratio higher than 0.80 and a density ratio higher than 0.20 were classified as overstorey families. Understorey families were families with a basal area ratio lower than 0.60 and a density ratio lower than 0.20. PRF showed only two overstorey families, while PPF forest had six and FWP five. Three families were placed in the intermediate storey in PRF, one in PRFa and two in PRFb. None of the other forest types showed any family in this category. Families such as the Chrysobalanaceae, Lecythidaceae, Sapotaceae and, Simaroubaceae, which belonged to the overstorey in FWP, occurred as understorey families in PRF.

Species composition

A species list with the species names, authorities, families and type of forest is given in appendix 2. Where species have only been determined to family level or merely assigned as different taxa, collection numbers are cited.

The list of species of trees ≥ 10 cm, ≥ 30 cm and ≥ 50 cm dbh and their phytosociological values are shown in Tables 4.18-4.26. The species were ranked in terms of cover value index and total basal area.

Density contribution

Peltogyne was the most abundant tree species in all diameter classes in PRF (Tables 4.18, 4.19, 4.23 and 4.26) contributing from 23% (trees ≥ 10 cm dbh), through 86% (trees ≥ 30 cm dbh) to 90% (trees ≥ 50cm dbh). In PPF this species occupied seventh place with 5% of trees (≥ 10 cm dbh) (Table 4.20), while *Tetragastris panamensis* and *Lecythis corrugata* were the most abundant trees together contributing 11% of the total number. In FWP, *Licania*

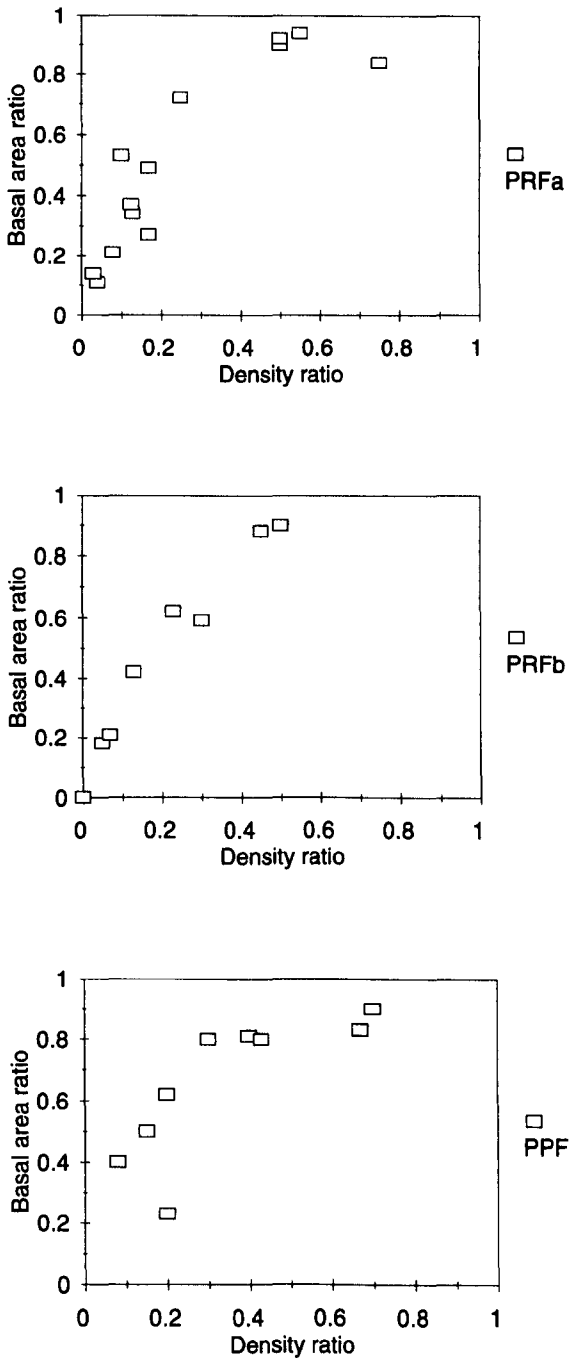
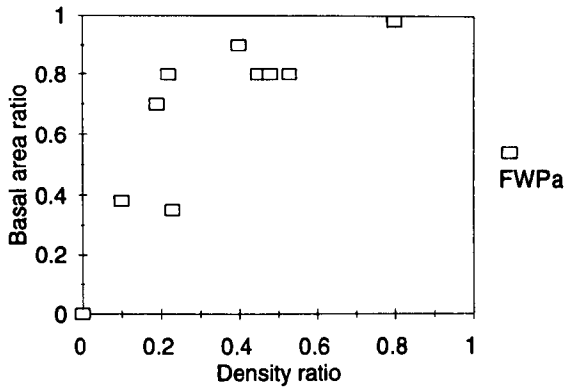


Figure 4.7. Relation between the ratio of basal area for tree > 30 cm dbh to that for trees > 10 cm dbh, and the same for density, from the 10 most important families in PRFa, PRFb and PPF.



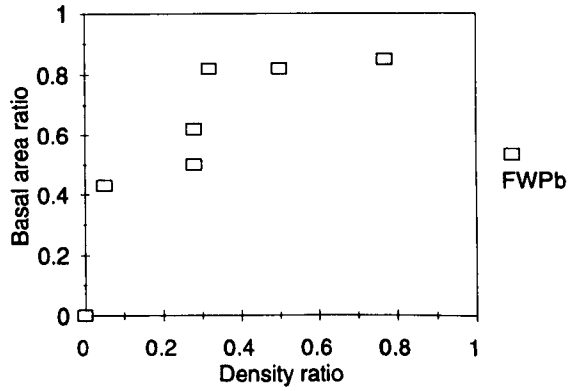


Figure 4.8. Relation between the ratio of basal area for tree > 30 cm dbh to that for trees > 10 cm dbh, and the same for density, from the 10 most important families in FWPa and FWPb.

Table 4.18. Species of trees ≥ 10 cm dbh occurring in three replicate 50 m x 50 m plots in PRF at trail 1 on Maracá Island, RR, Brazil with number of individuals (N), total basal area (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI). Species ranked by CVI.

Species	N	BA (m^2)	RD (%)	RDo (%)	CVI (%)
Peltogyne gracilipes	77	12.97	20.05	52.76	72.81
Ecclinusa guianensis	46	1.76	11.98	7.17	19.15
Pradosia surinamensis	36	1.78	9.38	7.23	16.60
Maximiliana maripa	28	1.60	7.29	6.52	13.81
Lecythis corrugata	31	1.06	8.07	4.30	12.38
Tabebuia uleana	28	0.92	7.29	3.73	11.02
Simarouba amara	13	0.99	3.39	4.01	7.39
Alseis longifolia	18	0.22	4.69	0.88	5.57
Picramnia cf. spruceana	11	0.14	2.86	0.56	3.43
Chomelia barbellata	9	0.23	2.34	0.93	3.27
Enterolobium schomburgkii	4	0.44	1.04	1.80	2.84
Himatanthus articulatus	7	0.16	1.82	0.66	2.48
Peltogyne paniculata	7	0.13	1.82	0.53	2.36
Chaunochiton kappleri	4	0.30	1.04	1.21	2.25
Pouteria reticulata	7	0.09	1.82	0.38	2.20
Swartzia grandifolia	4	0.09	1.04	0.38	1.42
Couepia paraensis	4	0.09	1.04	0.37	1.42
Pouteria surumuensis	3	0.15	0.78	0.59	1.37
Eugenia sp.	4	0.07	1.04	0.30	1.34
Licania apetala	1	0.26	0.26	1.06	1.32
Lonchocarpus sp.	4	0.06	1.04	0.25	1.29
Licania kunthiana	3	0.11	0.78	0.44	1.22
Apeiba schomburgkii	3	0.11	0.78	0.43	1.21
Vitex schomburgkiana	2	0.13	0.52	0.53	1.06
Duroia eriopila	3	0.05	0.78	0.19	0.97
Drypetes variabilis	2	0.05	0.52	0.20	0.72
Machaerium sp.	2	0.04	0.52	0.18	0.70
Pouteria hispida	2	0.03	0.52	0.13	0.65
MTN 3923	2	0.02	0.52	0.10	0.62
MTN 3733	2	0.02	0.52	0.09	0.61
Ormosia smithii	1	0.07	0.26	0.29	0.55
Ormosia sp.1	1	0.07	0.26	0.28	0.54
Faramea crassiloba	1	0.05	0.26	0.21	0.48
Guatteria schomburgkiana	1	0.05	0.26	0.20	0.47
Combretum sp.	1	0.04	0.26	0.16	0.42
MTN 3973	1	0.03	0.26	0.14	0.40
Eugenia cupulata	1	0.03	0.26	0.12	0.38
Astrocaryum aculeatum	1	0.03	0.26	0.12	0.38
Aspidosperma nitidum	1	0.02	0.26	0.10	0.36
Crepidospermum goudotianum	1	0.02	0.26	0.10	0.36
Abuta grandifolia	1	0.02	0.26	0.07	0.33
Byrsonima schomburgkiana	1	0.02	0.26	0.06	0.32
Ficus sp.	1	0.01	0.26	0.05	0.31
Pouteria cladantha	1	0.01	0.26	0.04	0.30
Lueheopsis duckeana	1	0.01	0.26	0.04	0.30
Faramea longifolia	1	0.01	0.26	0.04	0.30
Guapira sp.	1	0.01	0.26	0.03	0.30

Table 4.19. Species of trees ≥ 10 cm dbh occurring in three replicate 50 m x 50 m plots in PRF at Maracá House on Maracá Island, RR, Brazil with number of individuals (N), total basal area (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI). Species ranked by CVI.

Species	N	BA (m^2)	RD (%)	RDo (%)	CVI (%)
Peltogyne gracilipes	113	18.24	25.98	62.15	88.12
Zygia sp.2	53	1.94	12.18	6.61	18.80
Pradosia surinamensis	47	2.07	10.80	7.06	17.86
Eugenia cupulata	44	0.70	10.11	2.37	12.49
Cordia sellowiana	24	0.82	5.52	2.79	8.31
Zygia sp.1	11	1.19	2.53	4.05	6.58
Casearia ulmifolia	19	0.22	4.37	0.74	5.11
Alseis longifolia	16	0.27	3.68	0.94	4.61
Pouteria surumuensis	9	0.32	2.07	1.10	3.17
Apeiba schomburgkii	7	0.45	1.61	1.52	3.13
Chomelia barbellata	9	0.26	2.07	0.90	2.97
Ecclinusa guianensis	8	0.30	1.84	1.01	2.85
Hymenaea courbaril	9	0.23	2.07	0.78	2.85
MTN17	9	0.20	2.07	0.70	2.77
Rinorea brevipes	9	0.16	2.07	0.54	2.61
Tabebuia uleana	5	0.35	1.15	1.18	2.33
Zollernia grandifolia	1	0.33	0.23	1.14	1.37
Picramnia cf. spruceana	4	0.05	0.92	0.18	1.10
MTN342	2	0.18	0.46	0.63	1.09
Ocotea fasciculata	4	0.05	0.92	0.16	1.08
Himatanthus articulatus	2	0.13	0.46	0.44	0.90
Alexa canaracunensis	1	0.19	0.23	0.63	0.86
Ficus sp.1	1	0.18	0.23	0.62	0.85
Bauhinia ungulata	3	0.04	0.69	0.15	0.84
Couepia sp.	3	0.04	0.69	0.13	0.82
Combretum sp.	2	0.04	0.46	0.13	0.59
MTN389	2	0.04	0.46	0.13	0.59
Bauhinia sp.	2	0.03	0.46	0.11	0.57
Erythroxylum anguifugum	2	0.02	0.46	0.08	0.54
Amaioua corymbosa	2	0.02	0.46	0.07	0.53
MTN225	1	0.05	0.23	0.17	0.40
Agonandra silvatica	1	0.05	0.23	0.16	0.39
Genipa americana	1	0.03	0.23	0.10	0.33
Peltogyne paniculata	1	0.03	0.23	0.10	0.33
Duroia eriopila	1	0.03	0.23	0.10	0.33
Swartzia grandifolia	1	0.02	0.23	0.09	0.31
Duguetia lucida	1	0.02	0.23	0.05	0.28
MTN414	1	0.02	0.23	0.05	0.28
Xanthoxylum aff. rigidum	1	0.01	0.23	0.05	0.28
MTN224	1	0.01	0.23	0.04	0.27
Quiina cf. rhytidopus	1	0.01	0.23	0.03	0.26
Machaerium sp.	1	0.01	0.23	0.03	0.26

Table 4.20. Species of trees ≥ 10 cm dbh occurring in three replicate 50 m x 50 m plots in PPF at trail 1 on Maracá Island, RR, Brazil with number of individuals (N), total basal area (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI). Species ranked by CVI.

Species	N	BA (m^2)	RD (%)	RDo (%)	CVI (%)
Peltogyne gracilipes	16	4.98	4.68	20.05	24.73
Pradosia surinamensis	25	3.46	7.31	13.91	21.22
Ecclinusa guianensis	34	2.51	9.94	10.08	20.03
Tetragastris panamensis	37	1.50	10.82	6.05	16.87
Lecythis corrugata	37	1.37	10.82	5.50	16.32
Licania kunthiana	23	2.28	6.73	9.16	15.88
Maximiliana maripa	24	1.47	7.02	5.93	12.94
Simarouba amara	14	1.58	4.09	6.03	10.12
Pouteria reticulata	16	0.63	4.68	2.53	7.21
Brosimum lactescens	11	0.74	3.22	2.97	6.19
Couratari multiflora	3	0.94	0.88	3.78	4.66
Pouteria hispida	6	0.65	1.75	2.61	4.37
Himatanthus articulatus	7	0.31	2.05	1.25	3.29
Alseis longifolia	7	0.13	2.05	0.52	2.57
Drypetes variabilis	5	0.19	1.46	0.78	2.25
Amaioua corymbosa	6	0.07	1.75	0.26	2.02
Pouteria surumuensis	5	0.10	1.46	0.39	1.86
Aspidosperma nitidum	2	0.28	0.58	1.11	1.70
Astrocaryum aculeatum	4	0.13	1.17	0.51	1.68
Pouteria venosa	3	0.17	0.88	0.70	1.58
Ampelocera edentula	4	0.09	1.17	0.36	1.52
Guatteria schomburgkiana	3	0.14	0.88	0.58	1.46
Duguetia lucida	4	0.04	1.17	0.16	1.33
Enterolobium schomburgkii	2	0.18	0.58	0.72	1.31
Lindackeria paludosa	3	0.08	0.88	0.32	1.20
Duroia eriopila	3	0.05	0.88	0.21	1.08
Chomelia barbellata	1	0.16	0.29	0.65	0.94
Ocotea fasciculata	2	0.07	0.58	0.28	0.87
Oenocarpus bacaba	2	0.05	0.58	0.22	0.80
Exellodendron barbatum	2	0.05	0.58	0.19	0.77
Gustavia augusta	2	0.04	0.58	0.17	0.75
Machaerium sp.	2	0.04	0.58	0.17	0.75
Eugenia cupulata	2	0.04	0.58	0.16	0.74
Pouteria cladantha	1	0.11	0.29	0.44	0.73
Apeiba schomburgkii	2	0.03	0.58	0.13	0.72
Lueheopsis duckeana	2	0.03	0.58	0.12	0.70
Crepidospermum goudotianum	2	0.02	0.58	0.06	0.65
Couepia paraensis	1	0.04	0.29	0.15	0.44
Inga sp.3	1	0.03	0.29	0.14	0.43
MTN 3499	1	0.03	0.29	0.12	0.41
Eschweilera pedicellata	1	0.03	0.29	0.12	0.41
Trichilia cipo	1	0.02	0.29	0.09	0.38
MTN 3733	1	0.02	0.29	0.07	0.36
Abuta grandifolia	1	0.02	0.29	0.06	0.36
MTN 3923	1	0.01	0.29	0.05	0.34
Ouratea castaneaefolia	1	0.01	0.29	0.05	0.34
Byrsonima schomburgkiana	1	0.01	0.29	0.04	0.33
Mezilaurus itauba	1	0.01	0.29	0.04	0.33
Ascosmium tomentellum	1	0.01	0.29	0.04	0.33
Tabebuia uleana	1	0.01	0.29	0.04	0.33
Ryania speciosa	1	0.01	0.29	0.04	0.33
Chrysophyllum lucentifolium	1	0.01	0.29	0.04	0.33
Picramnia cf. spruceana	1	0.01	0.29	0.03	0.33
Licania apetala	1	0.01	0.29	0.03	0.33
Cheiloclinum cognatum	1	0.01	0.29	0.03	0.32

Table 4.21. Species of trees ≥ 10 cm dbh occurring in three replicate 50 m x 50 m plots in FWP at trail 1 on Maracá Island, RR, Brazil with number of individuals, total basal area (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI). Species ranked by CVI.

Species	N	BA (m^2)	RD (%)	RDo (%)	CVI (%)
Licania kunthiana	35	4.13	11.33	20.23	31.55
Ecclinusa guianensis	34	2.90	11.00	14.24	25.24
Pradosia surinamensis	25	3.28	8.09	16.08	24.17
Maximiliana maripa	18	1.19	5.83	5.82	11.65
Lecythis corrugata	21	0.86	6.80	4.20	10.99
Tetragastris panamensis	12	1.22	3.88	5.97	9.86
Himatanthus articulatus	19	0.68	6.15	3.34	9.49
Pouteria hispida	12	1.10	3.88	5.38	9.26
Simarouba amara	5	0.95	1.62	4.64	6.26
Guatteria schomburgkiana	11	0.31	3.56	1.54	5.10
Brosimum lactescens	7	0.55	2.27	2.69	4.96
Duguetia lucida	11	0.15	3.56	0.73	4.29
Ocotea fasciculata	7	0.37	2.27	1.82	4.09
Drypetes variabilis	7	0.24	2.27	1.19	3.46
Couratari multiflora	1	0.58	0.32	2.85	3.18
Crepidospermum goudotianum	8	0.11	2.59	0.52	3.11
Astrocaryum aculeatum	6	0.21	1.94	1.03	2.97
Duroia eriopila	7	0.10	2.27	0.47	2.74
Amaioua corymbosa	7	0.08	2.27	0.38	2.65
Pouteria surumuensis	6	0.13	1.94	0.65	2.59
Guatteria sp.	3	0.24	0.97	1.17	2.14
Lindackeria paludosa	5	0.08	1.62	0.38	2.00
Oenocarpus bacaba	4	0.12	1.29	0.57	1.87
Aspidosperma cf. eteanum	1	0.19	0.32	0.94	1.27
Pouteria reticulata	3	0.06	0.97	0.29	1.27
Ampelocera edentula	3	0.05	0.97	0.24	1.21
Ouratea castaneaefolia	3	0.03	0.97	0.17	1.14
Aniba hostmanniana	1	0.11	0.32	0.55	0.87
Exellodendron barbatum	2	0.04	0.65	0.19	0.84
MTN 3923	2	0.04	0.65	0.18	0.83
Ormosia sp.	2	0.03	0.65	0.15	0.80
Enterolobium schomburgkii	2	0.02	0.65	0.11	0.75
Tabebuia uleana	1	0.04	0.32	0.18	0.50
Apeiba schomburgkii	1	0.02	0.32	0.12	0.45
Faramea crassiloba	1	0.02	0.32	0.11	0.43
Pouteria venosa	1	0.02	0.32	0.09	0.41
Machaerium sp.	1	0.02	0.32	0.08	0.41
Alseis longifolia	1	0.02	0.32	0.08	0.40
Inga sp.1	1	0.01	0.32	0.06	0.38
Sloanea garkeana	1	0.01	0.32	0.06	0.38
Maytenus guianensis	1	0.01	0.32	0.06	0.38
Maprounea guianensis	1	0.01	0.32	0.05	0.38
Lueheopsis duckeana	1	0.01	0.32	0.05	0.37
Agonandra silvatica	1	0.01	0.32	0.05	0.37
Sloanea guianensis	1	0.01	0.32	0.05	0.37
Eugenia cupulata	1	0.01	0.32	0.04	0.37
Ryania speciosa	1	0.01	0.32	0.04	0.36
Hymenaea courbaril	1	0.01	0.32	0.04	0.36
MTN 3141	1	0.01	0.32	0.04	0.36
Ormosia smithii	1	0.01	0.32	0.04	0.36
Quiina cf. rhytidopus	1	0.01	0.32	0.04	0.36

Table 4.22. Species of trees ≥ 10 cm dbh occurring in three replicate 50 m x 50 m plots in FWP (Thompson *et al.*'s unfelled plots 1992a) on Maracá Island, RR, Brazil with number of individuals (N), total basal area (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI). Species ranked by CVI.

Species	N	BA (m^2)	RD (%)	RDo (%)	CVI (%)
Licania kunthiana	22	3.35	6.45	18.63	25.08
Brosimum lactescens	23	2.07	6.74	11.51	18.26
Pouteria hispida	24	1.63	7.04	9.06	16.10
Tetragastris panamensis	12	1.61	3.52	8.97	12.49
Astrocaryum aculeatum	25	0.88	7.33	4.92	12.25
Duguetia lucida	27	0.44	7.92	2.47	10.39
Lecythis corrugata	15	0.76	4.40	4.21	8.60
Crepidospermum goudotianum	15	0.16	4.40	0.92	5.32
Ficus sp.1	1	0.88	0.29	4.88	5.18
Himatanthus articulatus	12	0.25	3.52	1.39	4.91
Clarisia racemosa	3	0.65	0.88	3.64	4.52
Pouteria surumuensis	6	0.45	1.76	2.49	4.25
Duroia eriopila	10	0.23	2.93	1.25	4.19
Lindackeria paludosa	11	0.12	3.23	0.65	3.88
Pinzona coriacea	8	0.23	2.35	1.30	3.65
Alseis longifolia	3	0.46	0.88	2.53	3.41
Pouteria ? torta	5	0.27	1.47	1.52	2.98
Pouteria venosa	7	0.13	2.05	0.72	2.77
Ecclinusa guianensis	5	0.23	1.47	1.28	2.74
Cordia sellowiana	5	0.20	1.47	1.12	2.59
Guatteria schomburgkiana	5	0.18	1.47	0.98	2.45
Simarouba amara	4	0.22	1.17	1.25	2.42
Sloanea garkeana	6	0.11	1.76	0.61	2.37
DS 628	1	0.33	0.29	1.85	2.14
Apeiba schomburgkii	5	0.11	1.47	0.60	2.07
Guettarda spruceana	5	0.07	1.47	0.41	1.88
Eugenia sp.	4	0.08	1.17	0.44	1.62
Aspidosperma cf. eteanum	4	0.07	1.17	0.40	1.57
Didymopanax morototoni	3	0.12	0.88	0.65	1.53
Mezilaurus itauba	4	0.06	1.17	0.32	1.49
Rudgea crassiloba	4	0.05	1.17	0.26	1.43
Rollinia exsucca	3	0.06	0.88	0.35	1.23
Swartzia dipetala	1	0.16	0.29	0.88	1.18
Ouratea castaneaefolia	3	0.05	0.88	0.28	1.16
Xylopia frutescens	3	0.05	0.88	0.27	1.15
Ocotea fasciculata	2	0.09	0.59	0.52	1.11
Guatteria sp.	2	0.08	0.59	0.42	1.01
Myrcia cf. splendens	2	0.07	0.59	0.41	1.00
Faramea sp.1	2	0.05	0.59	0.31	0.89
Pradosia surinamensis	2	0.05	0.59	0.30	0.89
Lueheopsis duckeana	2	0.05	0.59	0.30	0.88
Ampelocera edentula	2	0.05	0.59	0.27	0.85
Ormosia coarotada	1	0.09	0.29	0.50	0.79
Amaioua corymbosa	2	0.03	0.59	0.18	0.77
Inga sp.1	2	0.03	0.59	0.18	0.76
Chrysophyllum argenteum	2	0.03	0.59	0.15	0.73
DS 535	2	0.03	0.59	0.15	0.73
Casearia sylvestris	2	0.02	0.59	0.13	0.72
Dialium guianense	1	0.07	0.29	0.42	0.71
Maximiliana maripa	1	0.06	0.29	0.36	0.65
Trichilia sp.	1	0.06	0.29	0.34	0.63
Cassia moschata	1	0.05	0.29	0.28	0.57
DS 180	1	0.04	0.29	0.25	0.55
Astronium lecointei	1	0.04	0.29	0.22	0.51
Cecropia sp.	1	0.04	0.29	0.22	0.51
Chrysophyllum sparsiflorum	1	0.02	0.29	0.14	0.43
Hippocratea volubilis	1	0.02	0.29	0.11	0.40
DS 453	1	0.02	0.29	0.10	0.40
Ocotea sandwithii	1	0.02	0.29	0.08	0.38
Cupania sp.	1	0.01	0.29	0.08	0.37
Protium tenuifolium	1	0.01	0.29	0.07	0.36
Machaerium sp.	1	0.01	0.29	0.07	0.36
Virola cf. sebifera	1	0.01	0.29	0.07	0.36
DS 177	1	0.01	0.29	0.07	0.36
Arrabidea conjugata	1	0.01	0.29	0.06	0.35
R 5645	1	0.01	0.29	0.05	0.34
Ryania speciosa	1	0.01	0.29	0.05	0.34
DS 210	1	0.01	0.29	0.05	0.34
Chomelia barbellata	1	0.01	0.29	0.05	0.34
Combretum sp.	1	0.01	0.29	0.05	0.34

Table 4.23. Species of trees ≥ 30 cm dbh occurring in three replicate 50 m x 50 m plots in each of two PRF sites, (a) at trail 1 and (b) at Maracá House on Maracá Island, RR, Brazil with number of individuals (N), total basal area (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI). Species ranked by CVI.

Species	N	BA (m^2)	RD (%)	RDo (%)	CVI (%)
PRFa					
Peltogyne gracilipes	46	12.35	54.12	72.06	126.17
Pradosia surinamensis	10	1.24	11.76	7.21	18.97
Ecclinusa guianensis	6	0.62	7.06	3.62	10.68
Simarouba amara	3	0.86	3.53	4.99	8.52
Lecythis corrugata	4	0.36	4.71	2.08	6.79
Maximiliana maripa	4	0.30	4.71	1.78	6.49
Enterolobium schomburgkii	3	0.37	3.53	2.18	5.71
Chaunochiton kappleri	2	0.27	2.35	1.58	3.93
Licania apetala	1	0.26	1.18	1.52	2.70
Vitex schomburgkiana	1	0.12	1.18	0.69	1.87
Tabebuia uleana	1	0.10	1.18	0.57	1.75
Chomelia barbellata	1	0.08	1.18	0.45	1.63
Licania kunthiana	1	0.07	1.18	0.42	1.60
Ormosia smithii	1	0.07	1.18	0.42	1.60
Himatanthus articulatus	1	0.07	1.18	0.41	1.50
PRFb					
Peltogyne gracilipes	55	16.48	62.50	77.69	140.19
Zygia sp.2	9	0.87	10.23	4.10	14.32
Pradosia surinamensis	6	0.91	6.82	4.31	11.13
Zygia sp.1	5	1.00	5.68	4.71	10.40
Tabebuia uleana	2	0.29	2.27	1.36	3.63
Apeiba schomburgkii	2	0.20	2.27	0.97	3.24
Zollernia grandifolia	1	0.33	1.14	1.58	2.71
Alexa canaracunensis	1	0.19	1.14	0.88	2.01
Ficus sp.1	1	0.18	1.14	0.86	2.00
MTN342	1	0.17	1.14	0.81	1.94
Cordia sellowiana	1	0.17	1.14	0.80	1.93
Chomelia barbellata	1	0.11	1.14	0.53	1.67
Himatanthus articulatus	1	0.11	1.14	0.53	1.66
Ecclinusa guianensis	1	0.10	1.14	0.48	1.62
Pouteria surumuensis	1	0.08	1.14	0.40	1.54

Table 4.24. Species of trees ≥ 30 cm dbh occurring in three replicate 50 m x 50 m plots in PPF at trail 1 on Maracá Island, RR, Brazil with number of individuals (N), total basal area (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI). Species ranked by CVI.

Species	N	BA (m^2)	RD (%)	RDo (%)	CVI (%)
PPF					
Peltogyne gracilipes	11	4.85	10.89	25.93	36.82
Pradosia surinamensis	14	3.15	13.86	16.81	30.67
Ecclinusa guianensis	16	1.94	15.84	10.36	26.21
Licania kunthiana	12	1.92	11.88	10.29	22.17
Simarouba amara	10	1.46	9.90	7.79	17.69
Lecythis corrugata	6	0.59	5.94	3.15	9.09
Tetragastris panamensis	5	0.75	4.95	4.02	8.97
Maximiliana maripa	6	0.47	5.94	2.50	8.44
Couratari multiflora	2	0.90	1.98	4.81	6.79
Brosimum lactescens	3	0.60	2.97	3.21	6.18
Pouteria hispida	3	0.53	2.97	2.86	5.83
Pouteria reticulata	3	0.36	2.97	1.94	4.91
Aspidosperma nitidum	2	0.28	1.98	1.48	3.46
Himatanthus articulatus	2	0.20	1.98	1.07	3.05
Drypetes variabilis	2	0.17	1.98	0.89	2.87
Enterolobium schomburgkii	1	0.17	0.99	0.91	1.90
Chomelia barbellata	1	0.16	0.99	0.86	1.85
Pouteria cladantha	1	0.11	0.99	0.59	1.58
Pouteria venosa	1	0.10	0.99	0.54	1.53

Table 4.25. Species of trees ≥ 30 cm dbh occurring in three replicate 50 m x 50 m plots in each of two FWP, (a) at trail 1 and (b) Thompson *et al's* (1992) unfelled plots on Maracá Island, RR, Brazil with number of individuals (N), total basal area (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI). Species ranked by CVI.

Species	N	BA (m^2)	RD (%)	RDo (%)	CVI (%)
FWPa					
Licania kunthiana	19	3.42	21.59	23.57	45.17
Ecclinusa guianensis	19	2.35	21.59	16.20	37.79
Pradosia surinamensis	14	2.92	15.91	20.13	36.04
Tetragastris panamensis	8	1.17	9.09	8.08	17.17
Pouteria hispida	5	0.88	5.68	6.06	11.75
Simarouba amara	4	0.93	4.55	6.44	10.98
Maximiliana maripa	6	0.47	6.82	3.27	10.09
Brosimum lactescens	3	0.45	3.41	3.12	6.53
Lecythis corrugata	3	0.44	3.41	3.05	6.46
Couratari multiflora	1	0.58	1.14	4.01	5.15
Ocotea fasciculata	2	0.29	2.27	2.02	4.29
Aspidosperma cf. eteanum	1	0.19	1.14	1.32	2.46
Guatteria sp.	1	0.17	1.14	1.17	2.31
Himatanthus articulatus	1	0.11	1.14	0.78	1.92
Aniba hostmanniana	1	0.11	1.14	0.77	1.90
FWPb					
Licania kunthiana	12	3.03	19.05	26.60	45.65
Brosimum lactescens	11	1.58	17.46	13.85	31.31
Tetragastris panamensis	9	1.53	14.29	13.41	27.69
Pouteria hispida	9	1.16	14.29	10.19	24.48
Lecythis corrugata	4	0.39	6.35	3.46	9.81
Ficus sp.1	1	0.88	1.59	7.70	9.29
Clarisia racemosa	2	0.62	3.17	5.45	8.63
Pouteria surumuensis	3	0.35	4.76	3.10	7.86
Alseis longifolia	1	0.42	1.59	3.65	5.24
DS 628	1	0.33	1.59	2.91	4.50
Pouteria ? torta	1	0.17	1.59	1.45	3.04
Swartzia dipetala	1	0.16	1.59	1.39	2.98
Ecclinusa guianensis	1	0.13	1.59	1.13	2.72
Cordia sellowiana	1	0.11	1.59	1.01	2.60
Simarouba amara	1	0.11	1.59	0.94	2.53
Pinzona coriacea	1	0.10	1.59	0.86	2.45
Ormosia coarotada	1	0.09	1.59	0.78	2.37
Ocotea fasciculata	1	0.08	1.59	0.72	2.31
Didymopanax morototoni	1	0.08	1.59	0.71	2.30
Dialium guianense	1	0.07	1.59	0.66	2.25

Table 4.26. Species of trees ≥ 50 cm dbh occurring in three replicate 50 m x 50 m plots in PRF, PPF and FWP on Maracá Island, RR, Brazil, with number of individuals (N), total basal area (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI). Species ranked by CVI.

Species	N	BA (m^2)	RD (%)	RDo (%)	CVI (%)
PRFa					
Peltogyne gracilipes	21	8.94	91.30	90.87	182.18
Simarouba amara	1	0.64	4.35	6.47	10.82
Licania apetala	1	0.26	4.35	2.65	7.00
PRFb					
Peltogyne gracilipes	26	12.73	81.25	89.07	170.32
Zygia sp.1	2	0.56	6.25	3.91	10.16
Pradosia surinamensis	2	0.47	6.25	3.29	9.54
Zollernia grandifolia	1	0.33	3.13	2.34	5.46
Tabebuia uleana	1	0.20	3.13	1.40	4.52
PPF					
Peltogyne gracilipes	7	4.23	28.00	42.41	70.41
Pradosia surinamensis	6	2.25	24.00	22.55	46.55
Couratari multiflora	2	0.90	8.00	9.04	17.04
Licania kunthiana	2	0.54	8.00	5.42	13.42
Tetragastris panamensis	2	0.45	8.00	4.52	12.52
Ecclinusa guianensis	2	0.44	8.00	4.41	12.41
Simarouba amara	2	0.43	8.00	4.36	12.36
Brosimum lactescens	1	0.40	4.00	4.07	8.07
Pouteria hispida	1	0.32	4.00	3.23	7.23
FWPa					
Pradosia surinamensis	6	1.75	28.57	29.93	58.50
Licania kunthiana	6	1.51	28.57	25.70	54.27
Simarouba amara	3	0.81	14.29	13.75	28.03
Pouteria hispida	2	0.52	9.52	8.84	18.36
Couratari multiflora	1	0.58	4.76	9.93	14.69
Brosimum lactescens	1	0.24	4.76	4.17	8.93
Lecythis corrugata	1	0.23	4.76	3.94	8.70
Tetragastris panamensis	1	0.22	4.76	3.75	8.51
FWPb					
Licania kunthiana	6	2.27	35.29	36.00	71.29
Tetragastris panamensis	4	1.04	23.53	16.51	40.04
Brosimum lactescens	2	0.71	11.76	11.30	23.06
Ficus sp.1	1	0.88	5.88	13.95	19.83
Clarisia racemosa	1	0.45	5.88	7.20	13.08
Alseis longifolia	1	0.42	5.88	6.62	12.50
DS 628	1	0.33	5.88	5.27	11.15
Pouteria hispida	1	0.20	5.88	3.15	9.03

kunthiana (FWPa) and *Duguetia lucida* (FWPb) were the most common trees (≥ 10 cm dbh) with 11% and 8% of trees (Tables 4.21 and 4.22). With increasing minimum dbh to 30 cm or 50 cm, *Licania kunthiana* had the highest values of density in this forest type (Tables 4.25 and 4.26). *Ecclinusa guianensis, Lecythis corrugata* and *Pradosia surinamensis* were among the most abundant species in all forest types.

Basal area contribution

For all three diameter classes, *Peltogyne* had the highest basal area in PRF with values varying from an average of 57.5% (≥ 10 cm dbh) to 90% (≥ 50 cm dbh) of the total followed by *Pradosia surinamensis* (7%, ≥ 10 cm dbh) and *Simarouba amara* (6.5%, ≥ 50 cm dbh) (Tables 4.18, 4.19, 4.23 and 4.26). In contrast, in the FWP the most dominant species, *Licania kunthiana*, accounted for on average 19.5% (≥ 10 cm dbh) and 30% (≥ 50 cm), followed by *Pradosia surinamensis* with 16% and *Brosimum lactescens* 11% of the basal area for trees ≥ 10cm dbh (Tables 4.21, 4.22, 4.25 and 4.26). In PPF, *Peltogyne* was less abundant with 5% of stems ≥ 10 cm dbh, but it had some large trees (> 50 cm dbh) and with 20% of the total basal area was the most dominant species in this forest type also, followed by *Pradosia surinamensis* (14%) and *Ecclinusa guianensis* (10%) (Table 4.20). For trees ≥ 50 cm, *Peltogyne* had also the highest relative dominance value (42%) with *Pradosia surinamensis* in second place with 22% of the basal area (Table 4.26).

Species-area curve

The species-area curves showed a tendency to reach a plateau (Figure 4.9) in all PRF and PPF plots studied. However, in FWP this tendency was less clear. The mean number of tree (≥ 10 cm dbh) species was: PRF, 23; PPF, 32

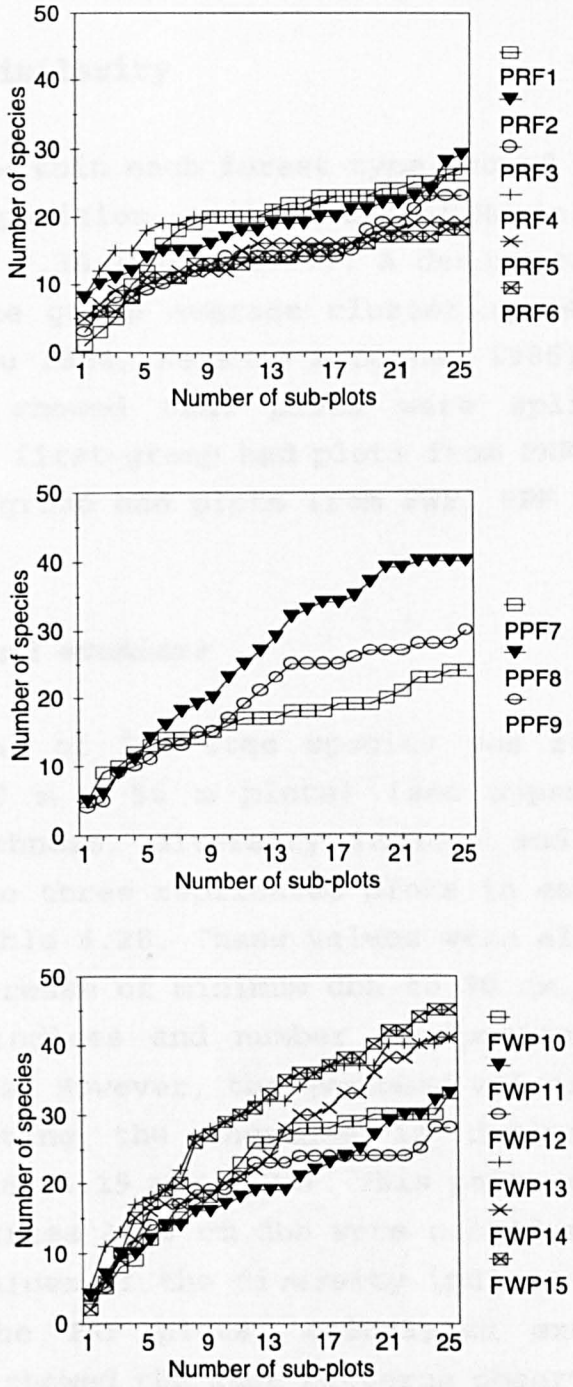


Figure 4.9. Species-curve area for trees (>=10 cm dbh) on each study plots in PRF, PPF, and FWP. Each curve follows the order of enumeration of the twenty-five 10-m x 10-m sub-plots.

and FWP 36.

Community similarity

Plots within each forest type showed high similarity in species composition, with values of Morisita's index always higher than 0.36 (Table 4.27). A dendrogram was produced by applying the group average clustering method (Greig-Smith 1983, Pielou 1984, Kershaw & Looney 1985) (Fig. 4.10). The dendrogram showed that plots were split into two main groups. The first group had plots from PRF, except PRF3, and the second group had plots from FWP, PPF and also PRF3.

Diversity and evenness

A total of 135 tree species was sampled in 3.75 ha (fifteen 50 m x 50 m plots) (see appendix 2). The mean species richness, diversity indices and evenness for the trees of the three replicated plots in each forest type are given in table 4.28. These values were always lower in PRF. With an increase of minimum dbh to 30 cm, the values of the diversity indices and number of species decreased in all forest types. However, the evenness values decreased only in PRF reflecting the increase in dominance of *Peltogyne* (Tables 4.18, 4.19 and 4.23). This pattern was even stronger when only trees ≥ 50 cm dbh were considered (Table 4.28).

The values of the diversity indices for trees (≥ 10 cm dbh) of the PRF plots, calculated excluding data from *Peltogyne*, showed the same patterns observed above, with PRF values always lower than the values found for the other forest types (Table 4.28). However, for trees ≥ 30 cm dbh when the *Peltogyne* data were excluded from the calculations of the Simpson index for PRF plots, some values increased showing that the *Peltogyne* interfered more with the species diversity owing to its greater dominance in this size class.

Table 4.27. Values of species similarity (Morisita's index) based on density of trees ≥ 10 cm dbh between plots from three forest types on Maracá Island, Brazil. Plots 1-6 are in PRF, plots 7-9 are in PPF and plots 10-15 are in FWP.

Plot															
12	1.00														
10	0.59	1.00													
11	0.56	0.67	1.00												
9	0.58	0.56	0.60	1.00											
7	0.50	0.68	0.63	0.53	1.00										
8	0.44	0.66	0.47	0.47	0.62	1.00									
1	0.33	0.34	0.31	0.36	0.36	0.46	1.00								
2	0.35	0.42	0.26	0.34	0.38	0.50	0.73	1.00							
3	0.46	0.60	0.46	0.46	0.50	0.69	0.40	0.45	1.00						
4	0.25	0.27	0.23	0.23	0.30	0.36	0.49	0.42	0.23	1.00					
5	0.18	0.20	0.23	0.16	0.27	0.31	0.41	0.39	0.23	0.61	1.00				
6	0.26	0.27	0.23	0.29	0.31	0.24	0.27	0.30	0.24	0.38	0.36	1.00			
13	0.35	0.43	0.40	0.31	0.42	0.36	0.24	0.20	0.28	0.17	0.12	0.17	1.00		
14	0.41	0.59	0.54	0.40	0.57	0.47	0.33	0.29	0.37	0.27	0.21	0.24	0.58	1.00	
15	0.44	0.56	0.52	0.41	0.49	0.39	0.25	0.22	0.32	0.19	0.17	0.16	0.58	0.65	1.00
	^	^	^	^	^	^	^	^	^	^	^	^	^	^	^
Plot	12	10	11	9	7	8	1	2	3	4	5	6	13	14	15

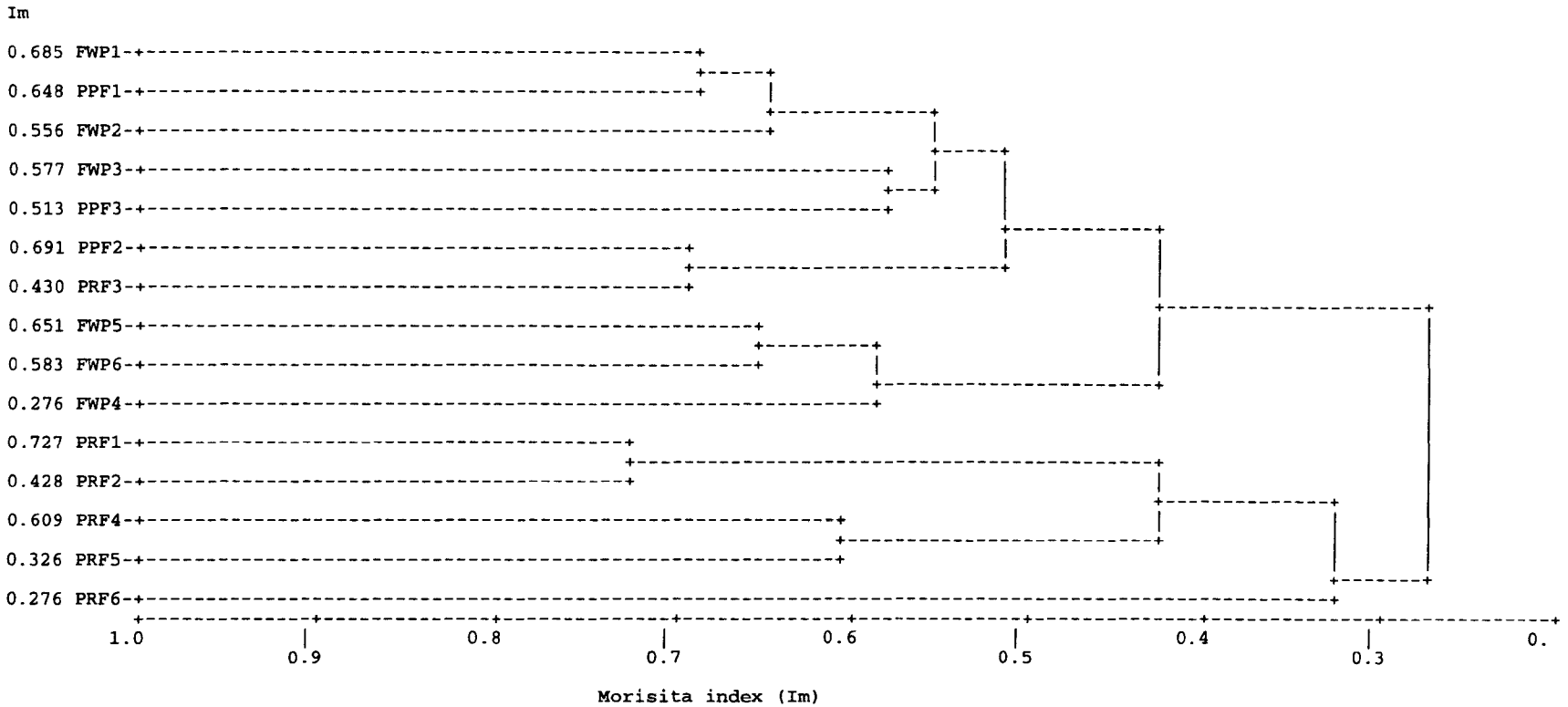


Figure 4.10. The dendrogram produced by applying group average clustering to the species similarity data between plots for trees ≥10 cm dbh from three different forest types on Maracá Island, Brazil.

Table 4.28. Mean species diversity for trees ≥ 10 cm dbh, ≥ 30 cm dbh and ≥ 50 cm dbh of three replicated 50-m x 50-m plots in three forest types on Maracá Island, Brazil. (standard deviation in parentheses)

Forest	1/Ds	H'	No. of spp.	Evenness*
Trees ≥ 10 cm dbh				
PRFa	9.11(1.91)	2.58(0.18)	26(2.52)	0.79(0.04)
PRFb	7.16(2.78)	2.27(0.43)	21(4.93)	0.74(0.09)
PPF	13.28(3.40)	2.86(0.27)	32(8.02)	0.84(0.02)
FWPa	17.64(1.58)	3.02(0.08)	31(2.89)	0.88(0.01)
FWPb	26.62(7.42)	3.37(0.14)	42(2.31)	0.90(0.02)
Trees ≥ 30 cm dbh				
PRFa	3.19(0.17)	1.49(0.12)	8(1.53)	0.72(0.02)
PRFb	2.57(0.98)	1.19(0.49)	7(3.79)	0.65(0.07)
PPF	10.08(4.10)	2.23(0.25)	13(2.08)	0.88(0.04)
FWPa	7.31(1.25)	1.95(0.20)	9(2.08)	0.88(0.02)
FWPb	9.15(4.94)	1.98(0.48)	10(4.16)	0.91(0.02)
Trees ≥ 50 cm dbh				
PRFa	0.85(0.74)	0.23(0.20)	2(0.58)	0.33(0.29)
PRFb	1.20(1.06)	0.47(0.45)	2(1.53)	0.47(0.41)
PPF	9.96(7.75)	1.45(0.50)	5(2.00)	0.92(0.09)
FWPa	5.33(1.63)	1.26(0.24)	4(1.00)	0.92(0.01)
FWPb	8.7(10.66)	1.21(0.49)	4(1.73)	0.90(0.15)

* H'/ln(number of species)

The rank-abundance diagrams for trees ≥ 10 cm dbh for each forest type showed that they had a similar pattern among forests, with a form of log-normal distribution (Fig. 4.11). However, in PRF the curves had more pronounced slopes, reflecting the differences in diversity and evenness from the other forest types.

Community structure

The 13 most important species in each forest type were classified as overstorey, understorey or intermediate species. This classification was based on the relation between the ratios for basal area and for density for trees ≥ 30 cm dbh to that for trees ≥ 10 cm dbh. The values of basal area and density for trees ≥ 10 cm dbh and ≥ 30 cm dbh for the 20 most important species (including all plots) are in tables 4.29, 4.30, 4.31 and 4.32. Species with a basal area ratio higher than 0.80 and density ratio higher than 0.20 were considered as overstorey species, while species that had ratio values lower than 0.60 for basal area and 0.20 for density were classified as understorey.

PRF showed the most important species split into two groups (overstorey and understorey) with similar numbers (Fig. 4.12). However, both PRFa and PRFb studied had two species placed between storeys. In contrast, FWP had the most important species within the overstorey category with very few as understorey species. PPF had a clear intermediate position among forests in relation to the species distribution within storey categories.

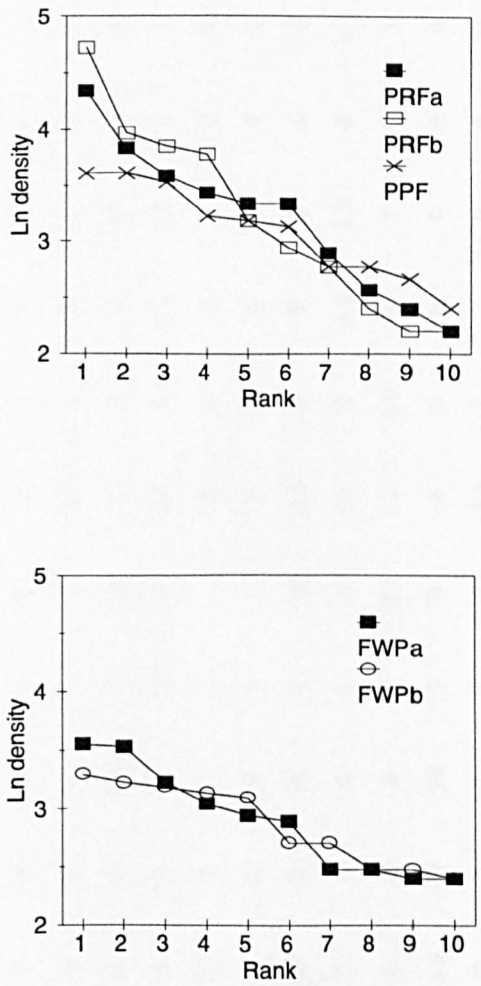


Figure 4.11. Ranked abundance (ln density) curves for the 10 most important species (>=10 cm dbh) in PRF, PPF and FWP.

Table 4.29. Tree (≥ 10 cm dbh) density per 0.25 ha plot for the 20 most important species in three forest types on Maracá Island, Roraima, Brazil.

	PRFa			PRFb			PPF			FWPa			FWPb		
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
Alseis longifolia	9	5	4	12	4	0	5	2	0	1	0	0	1	1	1
Astrocaryum aculeatum	0	0	1	0	0	0	0	0	4	2	2	2	8	9	8
Brosimum lactescens	0	0	0	0	0	0	1	0	10	2	5	0	8	11	4
Cordia sellowiana	0	0	0	0	0	24	0	0	0	0	0	0	3	2	0
Ecclinusa guianensis	1	4	41	6	1	1	12	6	16	8	11	15	1	1	3
Eugenia cupulata	0	0	0	42	2	0	1	1	0	0	0	1	0	0	0
Himatanthus articulatus	7	0	0	2	0	0	3	1	3	12	4	3	4	2	6
Lecythis corrugata	4	5	22	0	0	0	7	10	20	8	9	4	4	4	7
Licania kunthiana	0	0	3	0	0	0	2	1	20	9	16	10	6	11	5
Maximiliana maripa	17	7	4	0	0	0	1	22	1	10	1	7	0	1	0
Peltogyne gracilipes	28	28	21	36	27	50	6	6	4	0	0	0	0	0	0
Pouteria hispida	0	0	7	0	0	0	1	2	13	1	2	0	0	0	0
Pouteria reticulata	0	0	7	0	0	0	1	2	13	1	2	0	0	0	0
Pouteria surumuensis	1	1	1	7	1	1	4	1	0	4	1	1	5	1	0
Pradosia surinamensis	9	19	8	12	11	24	12	5	8	10	8	7	0	0	2
Simarouba amara	3	4	6	0	0	0	1	12	1	3	2	0	0	1	3
Tabebuia uleana	10	18	0	1	4	0	0	0	1	0	0	1	0	0	0
Tetragastris panamensis	0	0	0	0	0	0	19	4	14	1	1	10	2	3	7
Zygia sp1	0	0	0	7	3	1	0	0	0	0	0	0	0	0	0
Zygia sp2	0	0	0	0	0	53	0	0	0	0	0	0	0	0	0

Table 4.30. Tree (≥ 30 cm dbh) density per 0.25 ha plot for the 20 most important species in three forest types on Maracá Island, Roraima, Brazil.

	PRFa			PRFb			PPF			FWPa			FWPb		
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
Alseis longifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Astrocaryum aculeatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brosimum lactescens	0	0	0	0	0	0	1	0	2	1	2	0	6	1	1
Cordia sellowiana	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
Ecclinusa guianensis	0	0	6	0	1	0	6	2	8	6	4	9	0	0	1
Eugenia cupulata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Himatanthus articulatus	1	0	0	1	0	0	2	0	0	0	0	1	0	0	0
Lecythis corrugata	0	2	2	0	0	0	1	3	2	1	1	1	0	2	2
Licania kunthiana	0	0	1	0	0	0	2	1	9	7	6	6	3	7	2
Maximiliana maripa	2	2	0	0	0	0	1	5	0	2	0	4	0	0	0
Peltogyne gracilipes	14	15	17	14	15	26	4	6	1	0	0	0	0	0	0
Pouteria hispida	0	0	0	0	0	0	1	0	2	1	2	0	6	1	1
Pouteria reticulata	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0
Pouteria surumuensis	0	0	0	0	1	0	0	0	0	0	0	0	3	0	0
Pradosia surinamensis	1	5	4	1	3	2	4	3	7	6	6	2	0	0	0
Simarouba amara	1	1	1	0	0	0	1	8	1	3	1	0	0	0	1
Tabebuia uleana	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0
Tetragastris panamensis	0	0	0	0	0	0	3	1	1	0	1	7	2	2	5
Zygia sp1	0	0	0	4	1	0	0	0	0	0	0	0	0	0	0
Zygia sp2	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0

Table 4.31. Basal area (m^2) of trees (≥ 10 cm dbh) per 0.25 ha plot for the 20 most important species in three forest types on Maracá Island, Roraima, Brazil.

	PRFa				PRFb			PPF			FWPa				FWPb
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
Alseis longifolia	0.11	0.05	0.06	0.22	0.06	0.00	0.11	0.02	0.00	0.02	0.00	0.00	0.42	0.01	0.03
Astrocaryum aculeatum	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.13	0.07	0.07	0.08	0.31	0.29	0.29
Brosimum lactescens	0.00	0.00	0.00	0.00	0.00	0.00	0.40	0.00	0.20	0.11	0.34	0.00	0.91	0.29	0.29
Cordia sellowiana	0.00	0.00	0.00	0.00	0.00	0.82	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.05	0.00
Ecclinusa guianensis	0.01	0.09	1.66	0.17	0.10	0.03	0.85	0.32	1.33	0.83	0.72	1.35	0.01	0.05	0.17
Eugenia cupulata	0.00	0.00	0.00	0.67	0.02	0.00	0.03	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.00
Himatanthus articulatus	0.16	0.00	0.00	0.13	0.00	0.00	0.22	0.02	0.07	0.36	0.12	0.20	0.10	0.03	0.12
Lecythis corrugata	0.09	0.26	0.71	0.00	0.00	0.00	0.16	0.63	0.58	0.38	0.25	0.22	0.13	0.21	0.41
Licania kunthiana	0.00	0.00	0.11	0.00	0.00	0.00	0.18	0.16	1.93	1.28	1.62	1.22	0.44	2.17	0.74
Maximiliana maripa	0.97	0.42	0.21	0.00	0.00	0.00	0.11	1.30	0.07	0.63	0.05	0.51	0.00	0.06	0.00
Peltogyne gracilipes	2.97	5.84	4.16	5.88	7.22	5.14	1.21	3.61	0.17	0.00	0.00	0.00	0.00	0.00	0.00
Pouteria hispida	0.00	0.00	0.03	0.00	0.00	0.00	0.53	0.06	0.06	0.06	0.34	0.70	1.15	0.44	0.04
Pouteria reticulata	0.00	0.00	0.09	0.00	0.00	0.00	0.02	0.11	0.50	0.02	0.04	0.00	0.00	0.00	0.00
Pouteria surumuensis	0.06	0.06	0.03	0.23	0.08	0.01	0.08	0.02	0.00	0.09	0.02	0.02	0.39	0.05	0.00
Pradosia surinamensis	0.26	0.84	0.67	0.52	0.84	0.71	1.25	0.62	1.59	1.26	1.51	0.51	0.00	0.00	0.05
Simarouba amara	0.13	0.67	0.19	0.00	0.00	0.00	0.23	1.06	0.15	0.63	0.31	0.00	0.00	0.03	0.19
Tabebuia uleana	0.50	0.42	0.00	0.02	0.33	0.00	0.00	0.00	0.01	0.00	0.00	0.04	0.00	0.00	0.00
Tetragastris panamensis	0.00	0.00	0.00	0.00	0.00	0.00	0.83	0.15	0.52	0.01	0.11	1.09	0.34	0.36	0.91
Zygia sp1	0.00	0.00	0.00	0.99	0.19	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Zygia sp2	0.00	0.00	0.00	0.00	0.00	1.94	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 4.32. Basal area (m^2) of trees (≥ 30 cm dbh) per 0.25 ha plot for the 20 most important species in three forest types on Maracá Island, Roraima, Brazil.

	PRFa				PRFb			PPF			FWPa				FWPb
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
Alseis longifolia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.42	0.00	0.00
Astrocaryum aculeatum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Brosimum lactescens	0.00	0.00	0.00	0.00	0.00	0.00	0.40	0.00	0.20	0.11	0.34	0.00	0.91	0.29	0.29
Cordia sellowiana	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00
Ecclinusa guianensis	0.00	0.00	0.62	0.00	0.10	0.00	0.64	0.19	1.11	0.70	0.46	1.19	0.00	0.00	0.13
Eugenia cupulata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Himatanthus articulatus	0.07	0.00	0.00	0.11	0.00	0.00	0.20	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00
Lecythis corrugata	0.00	0.17	0.19	0.00	0.00	0.00	0.07	0.36	0.16	0.23	0.08	0.13	0.00	0.16	0.24
Licania kunthiana	0.00	0.00	0.07	0.00	0.00	0.00	0.18	0.16	1.58	1.15	1.20	1.08	0.34	2.07	0.61
Maximiliana maripa	0.16	0.14	0.00	0.00	0.00	0.00	0.11	0.36	0.00	0.15	0.00	0.32	0.00	0.00	0.00
Peltogyne gracilipes	2.71	5.58	4.06	5.06	7.00	4.41	1.14	3.61	0.11	0.00	0.00	0.00	0.00	0.00	0.00
Pouteria hispida	0.00	0.00	0.00	0.00	0.00	0.00	0.53	0.00	0.00	0.00	0.25	0.63	0.96	0.20	0.00
Pouteria reticulata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.26	0.00	0.00	0.00	0.00	0.00	0.00
Pouteria surumuensis	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.35	0.00	0.00
Pradosia surinamensis	0.18	0.51	0.54	0.17	0.58	0.16	1.04	0.57	1.53	1.12	1.44	0.36	0.00	0.00	0.00
Simarouba amara	0.09	0.64	0.13	0.00	0.00	0.00	0.23	1.08	0.15	0.63	0.31	0.00	0.00	0.00	0.11
Tabebuia uleana	0.10	0.00	0.00	0.00	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tetragastris panamensis	0.00	0.00	0.00	0.00	0.00	0.00	0.44	0.08	0.23	0.00	0.11	1.06	0.34	0.35	0.84
Zygia sp1	0.00	0.00	0.00	0.87	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Zygia sp2	0.00	0.00	0.00	0.00	0.00	0.87	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

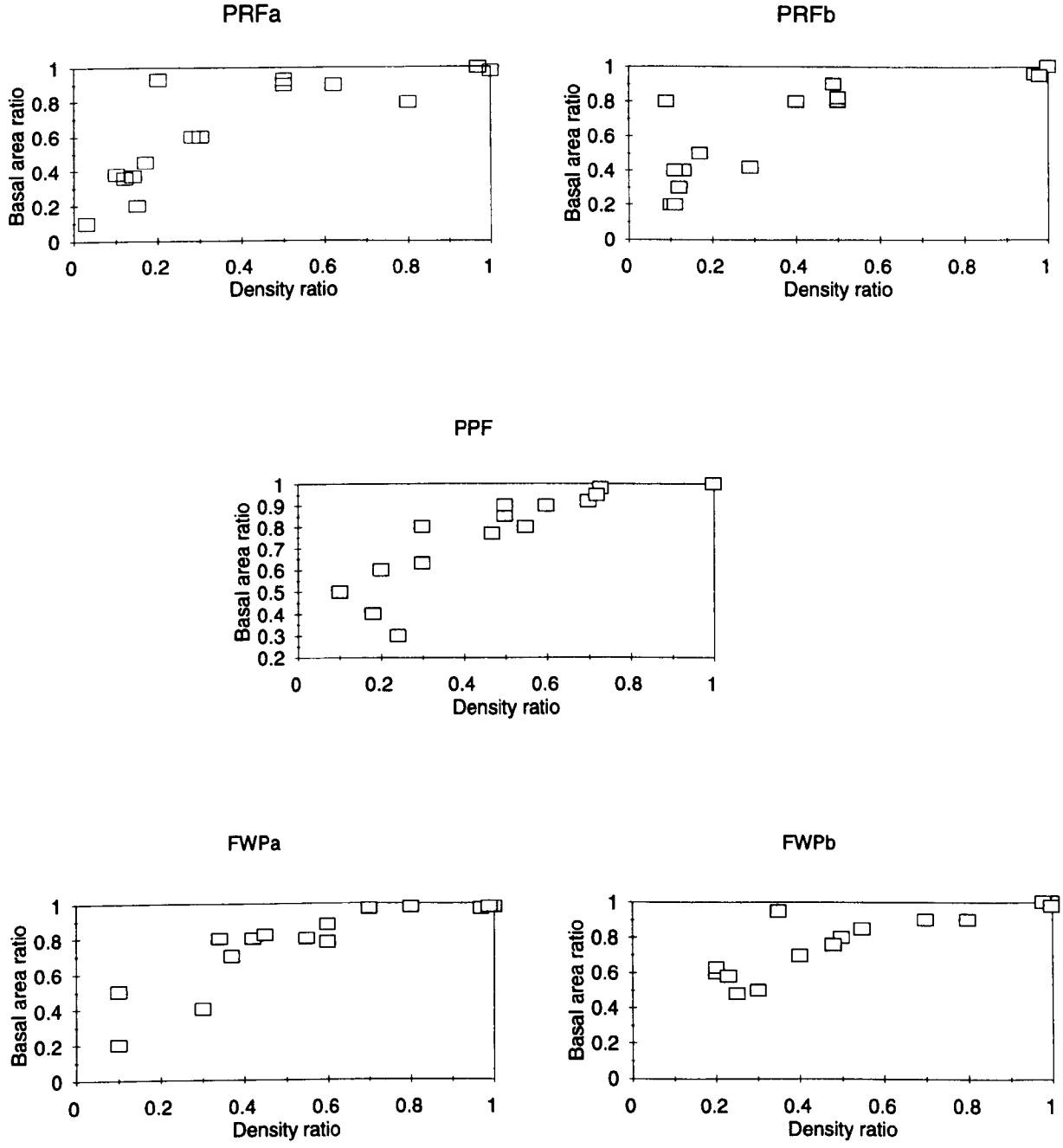


Figure 4.12. Relation between the ratio of basal area for trees > 30 cm dbh to that for trees > 10 cm dbh and the same for density for the 15 most important species in PRF, PPF and FWP.

DISCUSSION

PHYSICAL ENVIRONMENT

The surface soils of the plots are, in general, sandy, with a low percentage of clay, total phosphorus and exchangeable calcium and potassium. They can be considered among the poorest soils among Amazonian lowland evergreen rain forests (Thompson *et al.* 1992a). However, in most plots the values of available phosphorus are moderate, and of percentage base saturation are relatively high. Thompson *et al.* (1992a) found lower values for total nitrogen and exchangeable potassium on a volume basis in FWPb than the range of values recorded for tropical rain forests elsewhere. Statistically significant differences were found mainly between PRF soils and soils from FWP. Soils from PRF had a tendency to have more silt and be richer in nutrients than soils from FWP, with most obviously higher magnesium, and Mg/Ca quotients, Mg/total base quotients. Nortcliff & Robison (1989) pointed out that many of the soils underlying the PRF have the highest concentrations of exchangeable magnesium recorded on the Island. They also considered that PRF is frequently related to the lower undulating regions, with lower slopes and broad valley bottoms having poorer drainage. The data here support this view for magnesium. PRF seems to follow old drainage systems (see Chapter 3, Fig. 3.1) from NE to SW. However, it is important to note that although PRF can occur in poorly drained areas (Milliken & Ratter 1989, Furley & Ratter 1990) it is not restricted to these sites. On the contrary, most of PRF transects on Maracá reported by Milliken & Ratter (1989) were on well-drained soils, with the highest values (60%) of relative dominance of *Peltogyne* on a sandy and well-drained soil on the Fumaça trail. This forest type was never found on seasonally flooded areas on Maracá island. Data for the water table level for each plot in PRFa, PPF and FWPa measured from March 1992 (dry season) to August 1992 (wet

season) showed that although during the peak of the wet season the water table was always higher in the PRF it never reached the soil surface (D. Villela personal communication).

Available phosphorus has been reported to be negatively related to the abundance of the Caesalpiniaceae in the Korup forest in Cameroon (Gartlan *et al.* 1986), but this was not so on Maracá.

The higher concentrations of total nitrogen found in PRF may not be related to *Peltogyne*, since this species does not seem to have a nitrogen-fixing bacterial association (M Nascimento, personnal observation). The soil-vegetation relationship will be dealt with in more detail in Chapter 5.

FOREST STRUCTURE

The forest formation

The Maracá forests range from a type (found on the western tip of Maracá) which is similar to that of Central Amazonia to a floristically and structurally different type at the eastern end of the island (Milliken & Ratter 1989). According to RadamBrasil (1975) the forests of Maracá should be classified as "floresta estacional semidecidual" (semi-deciduous seasonal) at the eastern tip and "Floresta Densa" (evergreen forests) at the western end. However, the FWP of the eastern part of Maracá should be considered as a tropical lowland evergreen rain forest (*sensu* Whitmore 1984) rather than a semi-deciduous seasonal forest, since less than 6% of the trees are deciduous (Thompson *et al.* 1992a). On the other hand, semi-deciduous forests can occur in the eastern part of Maracá. Thompson *et al* (1994) found 45% of the trees to be deciduous in an area about 3 km north of the FWPb plots and this area was considered by them to be a small patch of semi-evergreen forest. It is important to note that *Peltogyne* did not occur there, although the PRF can also be classified (*sensus* Beard 1944) as semi-deciduous

forest, since at least 35% of the trees ≥ 10 cm dbh are deciduous with *Peltogyne* accounting for about two thirds of the deciduous individuals. If only trees ≥ 30 cm dbh are taken into account the PRF should be considered deciduous rather than semi-deciduous, since *Peltogyne* accounts for more than 54% of the trees in this dbh class and other deciduous trees such as *Cordia sellowiana, Chaunochiton kappleri, Enterolobium schomburgkii, Simarouba amara, Tabebuia uleana* occur frequently as a canopy component. Milliken & Ratter (1989) also suggested that some areas of *Peltogyne* forest should be classified as deciduous seasonal forest, since the proportion of deciduous trees exceeds two-thirds.

The PRF, a deciduous or semi-deciduous forest occurs in soils with more nutrients than the evergreen FWP, and reinforces the observations of Furley *et al.* (1988) and Ratter *et al.* (1973, 1978) and Thompson *et al.* (1994) that deciduous forests are associated with more nutrient-rich soils.

Vertical structure

The height of the canopy of the Maracá forests (20-35 m tall, with emergents reaching 40 m or more) is similar to that normally found for *terra firme* forest on the fringe of the Amazonian forest (Uhl 1982, Ratter *et al.* 1973 and 1978), but lower than values found for canopy height (30-40 m) in central (Prance *et al.* 1976, Takeuchi 1961) and eastern Amazonia (Almeida 1994). Although PRF showed a higher and more closed canopy than most of the forest types at the eastern part of the island, including the other two types of semi-evergreen forest studied by Thompson *et al.* (1994) and Milliken & Ratter (1989), a similar value for canopy height was found by Thompson *et al.* (1992a) for the FWPb.

Tree density

The Maracá forest types have values of tree density (≥ 10 cm dbh) ranging from 295 to 677 ha^{-1} (Tables 4.6 and 4.33), with the lowest value for FWPa at the eastern part of Maracá and the highest one for the PRF in the central area of the island. These values fall into the ranges of 285-859 trees ha^{-1} reported by Campbell *et al.* (1986), Gentry (1987) and Gentry (1988) for Amazonian forests. PRF values (401-677 trees ha^{-1}) are similar to those found for gallery forests in southern (416 ha^{-1}, Gibbs *et al.* 1980) and central Brazil (650 ha^{-1}, Felfili 1994) and for lowland rain forests in Africa (471 ha^{-1} Gartlan *et al.* 1986; 477 ha^{-1} Hart *et al.* 1989) and in southeast Asia (470 ha^{-1} Newbery *et al.* 1992). However, they are, in most of the cases, lower than the values reported by Proctor *et al.* (1983) for four sites in southeast Asia (615-778 trees ha^{-1}). The highest value (778 trees ha^{-1}) reported by them was for a heath forest.

Basal area

The basal area of the PRF's this study (mean 32.8, range 25.2-38.3 (PRFa), mean 36.7-43.1 (PRFb) was higher than the values for the other forest types on Maracá Island (Tables 4.5 and 4.33). Milliken & Ratter (1989) using the Point-centred quarter (PCQ) method also found the highest basal area values in forests dominated by *Peltogyne*. These values are at the higher end or above these reported by Pires & Prance (1985) for Amazonian forest (40 m^2 ha^{-1}, for exceptionally large forests) and Lamprecht (1972) for lowland rain forests in northern South America (30-40 m^2 ha^{-1}). They also are high compared with the range (23-37 m^2 ha^{-1}) for lowland rain forests in Africa (Dawkins 1959). On the other hand, the values found for the other semi-evergreen forests on Maracá are below the lower limit and fall into the range for open forests or vine forests (18-24 m^2 ha^{-1})

Table 4.33. A comparison of tree (≥10 cm) density, basal area, and number of tree species in the *Peltogyne*-rich forest with those from two other forests on Maracá Island. Data from: this study (*Peltogyne*-rich forests, PRFa and PRFb); Milliken & Ratter (1989) (PRFc and PRFd, Forest without *Peltogyne* at western tip of Maracá (FWPw) and semi-evergreen forest (SEF); and Thompson *et al* (1993) semi-evergreen forest (SEG).

	PRFa	PRFb	PRFc	PRFd	FWPw	SEG	SEF
Density (ha^{-1})	401	463	453	677	527	600	541
Basal area (m^2ha^{-1})	33	39	22	45	21	29	40
Tree species *	26	21	31	15	31	73	35

* Number of trees per: 0.25 ha (PRFa, PRFb and SEG); 0.17 ha (PRFc); per 0.12 ha (PRFd); 0.38 ha (FWPw) and 0.10 ha (SEF).

proposed by Pires & Prance (1985). For FWP's, including the plot FWPa, the values are at the lower end of the evergreen rain forest ranges as discussed by Thompson *et al.* (1992a). These authors suggested that the wide ranges for tree densities found by Milliken & Ratter (1989) for the forests at the east of Maracá may reflect different ages and degrees of disturbance as reported by Proctor & Miller (1994).

Lianas

The liana results (table 4.9) do not support Milliken & Ratter's (1989) view that the *Peltogyne* forest has a lack of lianas and that the occurrence of lianas on the smooth bark of *Peltogyne* is rare. About 50% of *Peltogyne* trees were supporting at least one liana. According to Putz (1984) the occurrence of one or more lianas often increases the chance of a tree having other lianas. So assessing the presence or absence of a liana per tree gives an idea of liana abundance in an area. Therefore, the data suggest that PRFa with 40% of trees with lianas has more lianas than the PPF (34%) and FWPa (22%). These values are lower than the values found by Balslev *et al.* (1987) (53%) for a tropical evergreen lowland rain forest in Amazônia, Ecuador, Campbell & Newbery (1993) (57%) for a lowland rain forest in Sabah, Malaysia and Putz *et al.* (1985) (44, 47 and 54%) for three other lowland rain forest sites in Sarawak, Malaysia. However, other authors have found similar proportions of trees supporting lianas to those found for PRF and PPF: Balslev *et al.* (1987) (31%) for a flooded Amazonian forest in Ecuador, Mori *et al.* (1983) (37.5%) for a moist forest in eastern Brazil, and Putz & Chai (1987) (33%) for a lowland rain forest at Lambir, Sarawak, Malaysia. Therefore, the value found for FWPa (22%) seems to be the least reported for lowland tropical rain forests.

Family composition

The Maracá forests are very similar in family composition, with the indices of similarity ranging from 64% to 85%, and even the similarity between the PRF and the FWP is high (70%). It is interesting to note that the lowest value (64%) of family similarity was found within the PRF (PRFa x PRFb). All these values can be considered very high for Amazonian forests. Campbell *et al.* (1986) studying a lowland evergreen rain forest in Amazonia found only 21% of family similarity between transects in the same forest type.

The main difference between PRF and FWP is that the Caesalpiniaceae are the most important family in the former, and occur with few species and number of individuals in the latter. The Sapotaceae were the second most important family in the PRF and the first in the FWP. The Sapotaceae were second to the Moraceae in the FWPb when data for all six plots of Thompson *et al.* (1992a) were used. Three of these plots were later felled and the data for the remaining plots, those used in this thesis, have Sapotaceae ranked first. These results are in agreement with Milliken & Ratter's (1989) data for forests at the eastern tip of Maracá. Other important features of the PRF are the absence or the low density and dominance of some families that are very important in the other forest types on Maracá, such as Annonaceae, Burseraceae, Chrysobalanaceae and Moraceae. Those families are in the list of the 11 most important families in the central Amazonian forest (Prance 1990). It is also noteworthy that families such as the Apocynaceae, Chrysobalanaceae, Lechythidaceae, and Palmae that were abundant in forests along the station trail system, including PRFa, were rare or did not occur at all in the PRFb in the Maracá House area. Despite this difference, Milliken & Ratter (1989) considered that the *Peltogyne* forests at the southern end of the Preguiça trail (near to

the PRFb plots) have a floristic composition more similar to the eastern FWP forests.

Although forest is continuous in the Amazon basin, the family importance varies from site to site, with the Leguminosae being the most important family in Amapá and Pará (Campbell *et al.* 1986), Leguminosae and Moraceae in Amazonian Ecuador (Valencia *et al.* 1994), Lecythidaceae in Manaus (Prance *et al.* 1976 and Rankin-de-Merona 1992), Moraceae and Myristicaceae in Beni, Bolivia (Boom 1986), Myristicaceae and Euphorbiaceae in Acre (Campbell *et al* 1986), Euphorbiaceae at the western end and Moraceae and Sapotaceae at the eastern end of Maracá (Milliken & Ratter 1989, Thompson *et al.* 1992a). Thompson *et al.* (1992a) emphasised that the Lecythidaceae, Leguminosae (*sensu lato*) , Myristicaceae and Euphorbiaceae did not contribute a high proportion of the species in their Maracá plots. However, in this study the plots in PRFa, PRFb, PPF and FWPa always showed the Lecythidaceae as the third or fourth most important family with the Caesalpiniaceae as the most important family in the PRF.

Species composition

The values of species similarity between plots within forest were usually high. However, in PRFa on the trail 1 the species similarity between plots PRF3 and PRF1 was 0.40 and between PRF3 and PRF2 was 0.45, while the value between PRF1 and PRF2 was higher (0.73). The relatively low values of species similarity for PRF3 may be related to its position close to the border of the PRF strip. For the PRFb the low values found between plots PRF6 and PRF4 (0.38) and PRF5 (0.36) can also be related to the island location of PRF6. However, Campbell (1994) also found low values of similarity between transects in Amazonian forests, with a maximum similarity of 0.21 in *terra firme* plots and 0.47 in the *várzea* forests. According to him, these values indicate

that there is probably no such thing as a "representative" small sample for any Amazonian forest.

Ecclinusa guianensis, Lecythis corrugata, Licania kunthiana, Maximiliana maripa, Pradosia surinamensis, Simarouba amara and Tetragastris paramensis are among the most important species on Maracá forests. However, *Peltogyne* showed the highest relative dominance values (62%) reported for Amazonian lowland forests. According to Milliken & Ratter (1989) *Pradosia surinamensis* can be considered one of the most important species in the forests at the eastern tip of Maracá. It is important to draw attention to the fact that species such as *Licania kunthiana* and *Tetragastris panamensis*, very common in PPF and FWP, occur with very low density and dominance in PRF. Another important point is the number of palms in PRF in relation to the FWP. In the former forest type, no palm occurred in the Maracá House plots, while in PRFa (station trail system) 28 individuals were recorded. However, most of these tree palms were located in plot PRF1 (n=17) suggesting that it might have suffered some disturbance. High densities of small individuals or trees of palm species such as *Astrocaryum aculeatum, Maximiliana maripa* and *Oenocarpus bacaba*, may be the result of higher degree of disturbance in these areas, since they are frequent and form dense populations in secondary forests (Kahn & Granville 1992). Proctor & Miller (1994) listed eight tree species that are known to be favoured by human disturbance (*Apeiba schomburgkii, Astrocaryum aculeatum, Genipa americana, Guazuma ulmifolia, Jacaranda copaia, Lindackeria paludosa, Maximiliana maripa* and *Simarouba amara*). Most of these species occur in PPF (six out of eight) and FWP (six out of eight, FWPa), while only three of these species occurred in PRFa and one in PRFb. However, as already mentioned in Chapter 3, no archaeological evidence or signs of charcoal or charred logs were found on the soil surface of these plots, excluding those of FWPb, although charcoal was found in all plots at 25 cm depth or more. Therefore, it is difficult to infer whether these

communities are a result of human disturbance or are natural.

The number of species (a total of 135 trees and lianas ≥ 10cm dbh) found in 3.75 ha (all the plots studied) on Maracá, and the species average of 49 species in 0.75 ha (PRF), 52 (PPF) and 56 (FWP) show that Maracá forests, especially the PRF, are in the lower range of the species richness for Amazonian lowland forests (range 60-300 species per ha, Campbell *et al* 1986 and Gentry 1988). Campbell *et al.* (1986) also found relatively low species richness in a lowland forest in the southeastern border of Amazonia (1500-1700 mm annual rainfall) with a range from 118 to 162 species per hectare. According to them these values are lower than the mean (174 species) for the ten comparable phytosociological studies conducted in Amazonia. They pointed out that their 1 ha transect would not have been sufficient to sample the species richness, since the species-area curve (all the transects combined) began to level off after about 1.5 ha and approached an asymptote at 3 ha. For the PRF, PPF and FWP, the species-area curves (Fig.4.9) suggest that the low species-richness is not a reflection of the insufficient area sampled. Other authors (Black *et al.* 1950, Ratter *et al.* 1973, Boom 1986, Gentry 1988), have also recorded low values for lowland Amazonian forests located on the fringe of the Amazonia, but the species richness of the PRF seems to be the lowest of the values already reported for a lowland rain forest in Amazonia.

CONCLUSIONS

The Maracá forests are among the poorest in tree species in Amazonia, and the *Peltogyne* forest is the least diverse of all. The dominance of *Peltogyne* is not related to disturbance or low-nutrient soils. PRF occurs in less disturbed areas with relatively nutrient-rich (especially magnesium) soils.

Chapter 5 Classification and ordination of the forest types

INTRODUCTION

Several methods of vegetation analysis have been used to describe plant communities (Orlóci 1978, Gauch 1982, Greig-Smith 1983, Pielou 1984, Kershaw & Looney 1985, Digby & Kempton 1987, Jongman *et al.* 1987, Kent & Coker 1992). The patterns of species distribution can help to indicate the environmental factors determining the plant community.

It is known that community variation is largely continuous (Gauch 1982). However, a classification of ecological communities, complemented by an ordination, provides a powerful approach to summarizing ecological data sets (Digby & Kempton 1987). Thus, multivariate analysis in its basic three levels: regression, classification and ordination, helps ecologists to identify physiognomic and floristic gradients and the possible factors responsible for them.

The present study reports an attempt to determine the relationships between the soils and the forest types studied on Maracá by the use of classification, ordination and regression techniques.

MATERIAL AND METHODS

THE DATA SET

Vegetation data (floristic, basal area and density) (Tables 4.17-24) and soil data (Table 4.2) were used: loss-on-ignition, pH, $N_{extractable}$, $P_{extractable}$, exchangeable bases (K^+,Na^+, Ca^{2+}, Mg^{2+}), Mg/Ca quotient, total acidity, CEC, silt, clay and sand.

FLORISTIC CLASSIFICATION

There are two methods of classification: hierarchical and non-hierarchical. This chapter will deal with only the former method. A hierarchical classification can be made using either an agglomerative or a divisive method.

In this study both hierarchical methods (agglomerative and divisive) were used to classify the forests.

Agglomerative hierarchical method ("Cluster Analysis")

According to Digby & Kempton (1987) the computational difficulties with divisive hierarchical methods have led to agglomerative hierarchical methods becoming popular. However, Gauch (1982) argued that the agglomerative procedures concentrate initial attention on the similarities between individuals and small groups, but the small distances between similar samples in these cases are more likely to be due to chance, and thus agglomerative techniques tend not to be robust. Greig-Smith (1983) pointed out another disadvantage in most agglomerative methods is that the fusion is based only on the information carried by the stands or groups being fused and does not take into account the information from stands with an absence of a particular species. Despite these disadvantages, the agglomerative methods can be useful and provide an objective preliminary classification when associated with an ordination (Digby & Kempton 1987).

A cluster analysis was carried out for both the basal area and the density data sets. For both analyses, dendrograms were produced, by applying the unweighted pair-group method which uses the arithmetic average (UPGMA) (Greig-Smith 1983, Pielou 1984). The Euclidean distance was used as a dissimilarity measure (Pielou 1984).

Divisive hierarchical method

The data set was also classified by two-way indicator analysis (TWINSPAN) (Hill 1979), a divisive method which produces groupings of both sites and species. This method, derived from the indicator-species analysis technique (Hill *et al.* 1975), constructs an ordered two-way table by identifying differential species. According to Hill (1979) a feature of this method is that first a classification of the samples is constructed, and then this classification is used to obtain a classification of the species according to their ecological preferences. The ordered two-way table is then produced when the two classifications are used together.

In this study, species with less than six individuals in all plots combined were excluded from the data set before the analyses. The final density data matrix had forty-eight species. For basal area data, only species with a minimum total of 0.10 m^2 in all the plots were used and the final matrix had sixty-six species. The removal of the minor species substantially reduced the calculations. In general, such species influence the results negligibly (Newbery 1991) and in most cases a data matrix including the most abundant species produces a satisfactory result (Greig-Smith 1971). Pseudospecies cut-levels were 0, 2, 5, 10 and 20 for density data and 0, 0.1, 0.5, 1.0 and 3.0 m^2 per plot for basal area data. All pseudospecies were given equal weighting. Thus, they reflected the real abundance of the species.

A TWINSPAN classification of all plots based on all species was also produced for trees ≥ 30 cm dbh.

FLORISTIC ORDINATION

Two ordination techniques were used: Principal Components Analysis (PCA) and Detrended Correspondence Analysis (DCA) (Hill & Gauch 1980). The analyses were made

by the CANOCO program version 3.10 (ter Braak 1988).

The choice of the model of PCA was based on the recommendations of Newbery (1991) for plots which show clear dominance, as the case of the PRF. A correspondence analysis model, DCA (Hill & Gauch 1980), was also used because it has been considered a better technique than PCA (Gauch 1982, Gauch *et al.* 1977) mainly because it eliminates, by detrending by segment, the two major problems of the correspondence analysis (CA) and PCA: 1) the compression of the ends of the first axis relative to the middle and 2) the second axis often has a quadratic relation with the first axis (the arch effect). Detrending by segment means that the first axis is divided into a number of segments and within each segment the second axis scores (site scores) are recalculated by subtracting their mean (Jongman *et al.* 1987).

PCA

The data were first logarithmically transformed to reduce the variance. According to Noy-Meir (1973) some form of standardisation is often required for ecological data matrices mainly to remove a dominant effect which is not of primary interest. Thus, for samples a standardisation by site norm was applied to remove differences in total abundance and species richness between plots (Orlóci 1978). Species were only centred and so they contributed to the outline of the components and groupings in proportion to the variances of their logarithmic abundances (Newbery 1991). There was no reason to apply here a standardisation technique which would give equal weight to all species (Noy-Meir *et al.* 1975). The consequence of this model (species centring and standardisation by site norm) is that those species which are dominant in many sites, especially if they are species poor, will have greatest weights (Noy-Meir *et al.* 1975).

Detrended Correspondence Analysis (DCA)

In this study a DCA detrending by segments was made for each data set using the default of the CANOCO program (ter Braak 1988). As for PCA, the data were log transformed prior to the analysis to reduce the variance.

ANALYSIS OF THE ENVIRONMENTAL VARIABLES

Soil data from all fifteen plots were analysed by a PCA. Phosphorus data were not available for PRF 4-6 plots and nitrogen for plots PRF 4-6 and FWP 13-15. Thus, the data used at those locations were the average of the values for the other plots.

The model used was standardisation by standard deviation. According to Jongman *et al.* (1987), the standardisation of variables is necessary if data were measured in differents units. Although PCA may not be appropriate as an ordination method for floristic data (Gauch 1982), it is still one of the best methods of analysis to ordinate samples based on environmental variables (Kent & Coker 1992).

A DCCA (a detrended form of the canonical correpondence analysis) was used to analyse the relationship between species abundance and soil variables. One or more of the variables which were highly correlated with each other and had a variance inflation factor (VIF) greater than twenty were excluded from the analyses (ter Braak 1988). Thus, only eight of the thirteen original variables were kept in the matrix in order to reduce redundancy. According to ter Braak (1986) the removal of variables that showed strong correlation with each other eliminates this multicollinearity problem and decreases only slightly the eigenvalues and species-environment correlations.

The Monte Carlo permutation test (ter Braak 1988, 1990) was applied as a statistical test for the significance of

the relationship between species and the environmental variables.

REGRESSION

The relationships between soil variables (loss-on-ignition, phosphorus, potassium, calcium, magnesium, total acidity, clay and silt) and the basal area of the ten most dominant species of the Maracá forests (*Brosimum lactescens, Ecclinusa guianensis, Lecythis corrugata, Licania kunthiana, Maximiliana maripa, Peltogyne gracilipes, Pradosia surinamensis, Pouteria hispida, Simarouba amara* and *Tetragastris panamensis*) were analysed by simple regressions calculated on linear, quadratic and cubic terms of a polynomial function of each soil variable concentration. An analysis of variance of regression was used to test for significance. The F-ratio was considered significant at $p \leq 0.05$.

RESULTS

FLORISTIC CLASSIFICATION

Cluster analyses

The dendrograms based on the basal area (Fig. 5.1) and density data (Fig. 5.2) for trees ≥ 10 cm dbh showed different paterns with the basal area dendrogram grouping splitting more distinguishable the plots. Two major groups were obtained: group 1, plots from FWP and PPF (excluding plot PPF8) and group 2, plots from the PRF and plot PPF8.

For trees ≥ 30 cm dbh, both dendrograms based on the basal area and density data produced very similar results to each other and split the plots into two major groups, as found for the basal area data for trees ≥10 cm dbh.

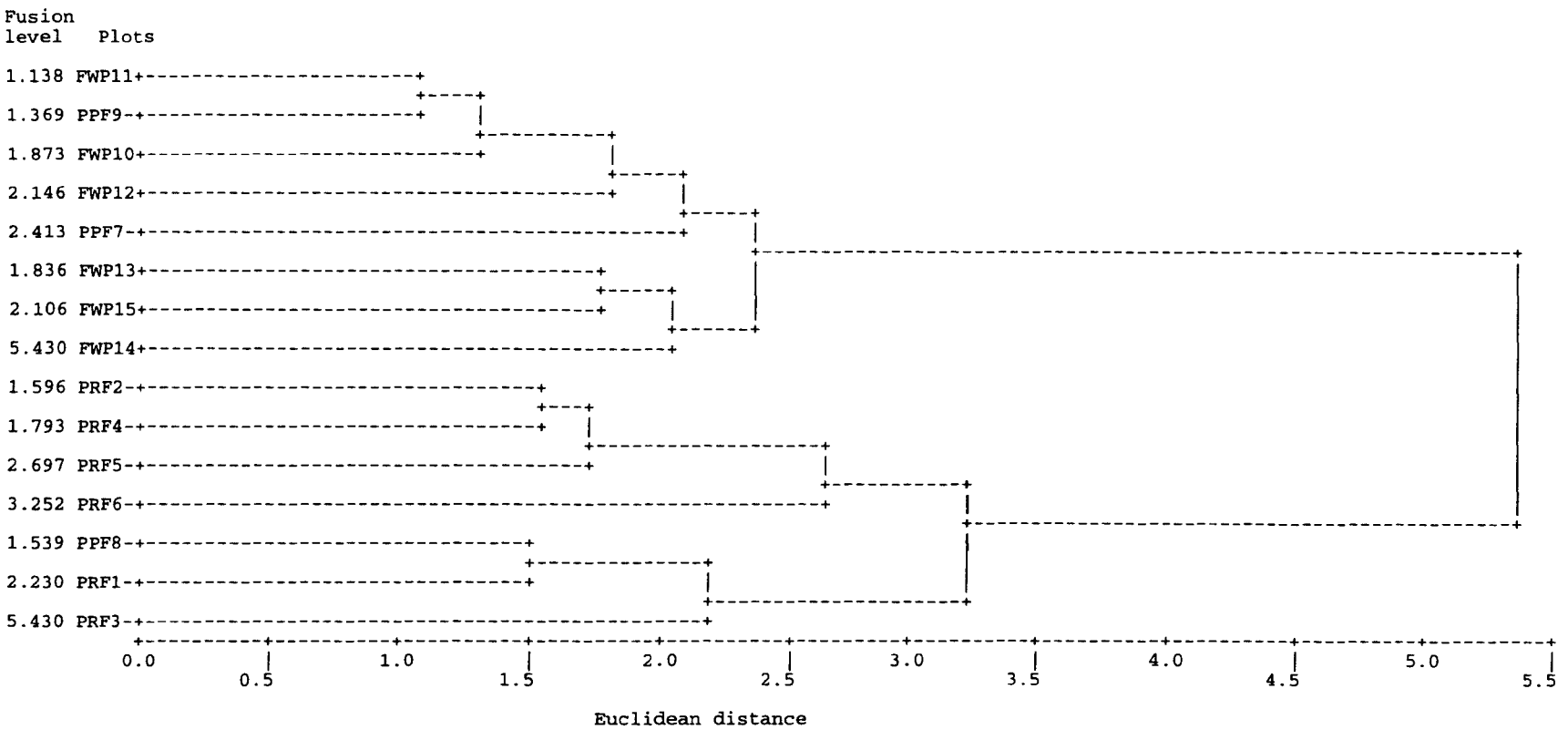


Fig. 5.1. The dendrogram produced by applying group average clustering to the basal area data between plots for trees ≥10 cm dbh from three different forest types on Maracá Island, Brazil.

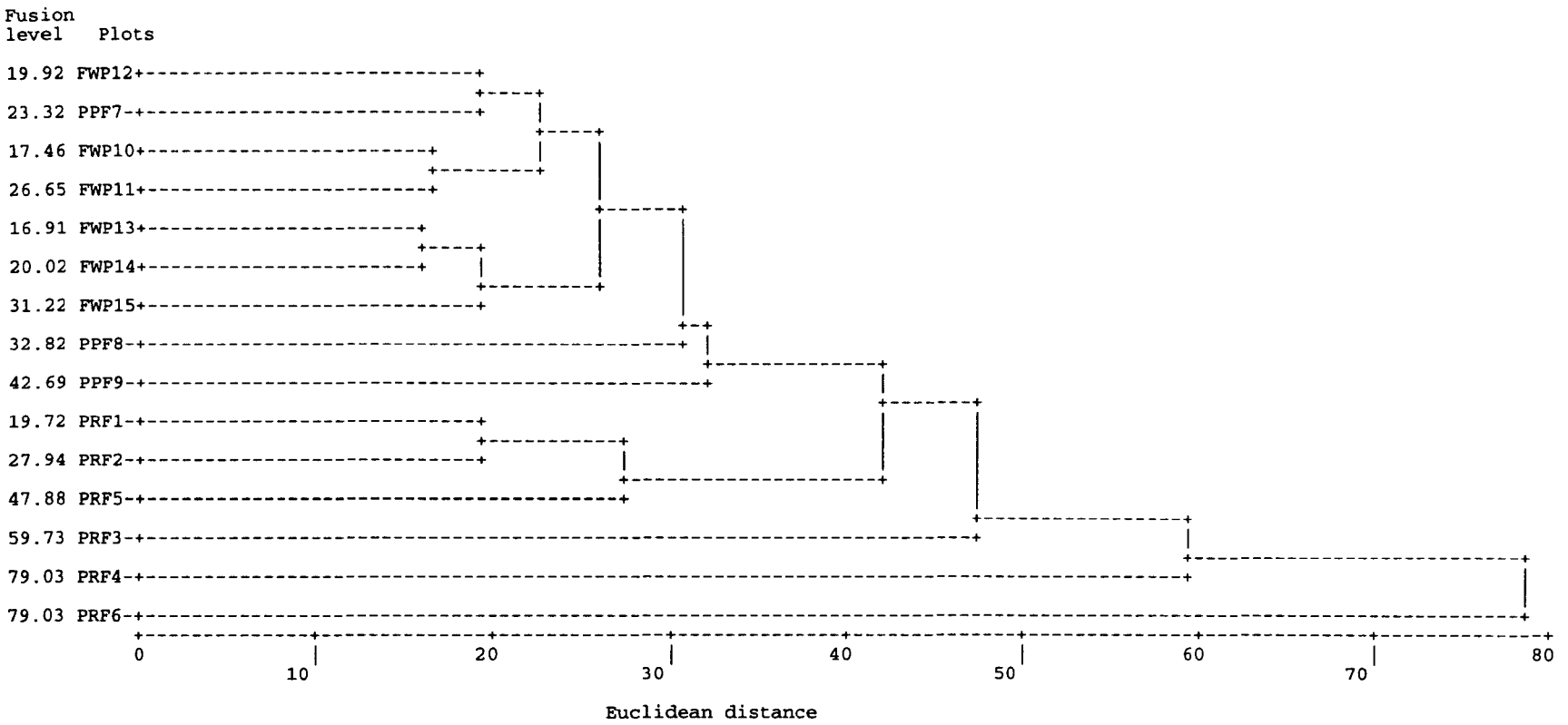


Fig. 5.2. The dendrogram produced by applying group average clustering to the density data between plots for trees ≥10 cm dbh from three different forest types on Maracá Island, Brazil.

TWINSPAN analysis

Only three distinct divisions were considered ecologically meaningful for plot groups considering the basal area data for trees ≥ 10 cm dbh. The eigenvalues for these three divisions were 0.45, 0.35, and 0.50. No misclassified or borderline plots occurred. The primary split was between PRF plots (excluding plot PRF3) and the rest of the plots (Table 5.1). Sequential divisions within the two primary groups were plot PRF6 split from the other PRF plots and plots from FWPb (FWP13-15) from the FWPa (FWP10-12) and PPF plots. The last division separated plots PPF8 and PRF3 from the FWPa plots and PPF7 plot. A better division of the plots, with plots from the same forest types split into the same classes was achieved for the basal area data of trees ≥ 30 cm dbh. Three distinct divisions were considered and their eigenvalues were 0.53, 0.46 and 0.47. As for trees ≥ 10 cm dbh, no misclassified or borderline plots occurred. The first division split plots into two major groups: 1) plots from PRF and plot PPF8, 2) plots from FWP and PPF7 and PPF9. In the second division, plot PRF6 was split from the first group, while plot FWP4 was split from the second one. The last division separated the plots PRF4 and PRF5 from the PRF group and plot FWP6 from the other group.

For the species groupings (trees ≥ 10 cm dbh), the two distinct associations detected at the first division were: the preferential species to the FWP and PPF plots such as *Astrocaryum aculeatum, Brosimum lactescens, Guatteria schomburgkiana, Lecythis corrugata, Licania kunthiana, Pouteria hispida,* and *Tetragastris panamensis*. The preferential species for PRF were mainly *Chomelia barbellata, Eugenia cupulata, Peltogyne, Pricamnia cf. spruceana,* and *Tabebuia uleana*. For the second division species such as *Clarisia racemosa, Didymopanax morototoni, Pinzona coriacea* and *Sloanea garkeana* showed a clear association with the FWPb plots. *Zygia sp.2* and the

Table 5.1. Twinspan two-way table based on the basal area data for trees ≥ 10 cm dbh from three different forest types on Maracá Island, Brazil. For the full names of the species see Appendix 2. In the columns for the fifteen plots '-' means that the species did not occur, and the values 1-5 refer to pseudospecies cut-level classes. Values in bold are non-preferential species.

	Species		Plots 111111 345201978312456	
27	Dryp	var	---22--2-1-----	00000
34	Oeno	bac	---1-1-1-------	00000
38	Cour	mul	-----332-------	00000
46	Anib	hos	---2-----------	00000
25	Pout	ret	----112121-----	00001
26	Lueh	duc	----1---11-----	00001
31	Aspi	nit	-------211-----	00001
48	Lica	ape	--------12-----	00001
24	Lica	kun	2434444222-----	0001
32	Guat	sch	-12122-2-1-----	0001
42	Oura	cas	--11111--------	0001
44	Guat	sp	--121----------	0001
37	Tetr	pan	223412332------	00100
41	Ampe	ede	1-11-111-------	00100
28	Astr	acu	2221112--1-----	001010
29	Pout	his	4213121311-----	001010
30	Crep	gou	111-11-111-----	001010
33	Pout	ven	111-1--21------	001010
36	Lind	pal	111-11-11------	001010
43	Bros	lac	342-2222-------	001010
47	Aspi	cf.	1112-----------	001010
50	Sloa	gar	111--1---------	001011
61	Didy	mor	111----------	001011
62	Pinz	cor	21----------	001011
63	Swar	dip	--2----------	001011
64	Clar	rac	2-2----------	001011
65	Pout	?	--2----------	001011
66	DS	628	--2----------	001011
4	**Lecy**	**cor**	**222222323312---**	**0011**
35	**Amai**	**cor**	**-1111-111-----1**	**0011**
40	**Dugu**	**luc**	**21211111------1**	**0011**
3	**Eccl**	**gui**	**112433432411221**	**010**
9	**Sima**	**ama**	**-12-32224223---**	**010**
10	**Maxi**	**mar**	**-1-331124232---**	**010**
12	**Hima**	**art**	**112222121-2-2--**	**011**
18	**Duro**	**eri**	**112111-11111--1**	**011**
21	**Mach**	**sp**	**-1--1-11---1--1**	**011**
39	**Ocot**	**fas**	**-11-12-1----11-**	**011**
2	**Prad**	**sur**	**--1344443323333**	**1000**
19	Pout	cla	--------2-1----	1000
23	Coue	par	--------11---1-	1000
15	Ente	sch	---1-12---22---	1001
22	Chau	kap	---------211---	1001
8	Pout	sur	21-111-11111211	101
17	Euge	sp	1-1-------11---	1100
56	Ficu	spl	--3----------2-	1100
58	Cord	sel	21----------3	1100
1	Pelt	gra	------245545555	1101
7	Alse	lon	211-1--2112121-	1101
13	Apei	sch	111-1--11-1122-	1101
20	Euge	cup	---1---11--131-	1101
16	Picr	cf.	-------1--11-11	1110
45	Hyme	cou	-----1------112	1110
59	Zygi	sp2	--------------4	1110
60	MTN	342	--------------2	1110
51	Zygi	spl	------------321	111100
53	Case	ulm	------------121	111100
5	Tabe	ule	---1--1---2212-	111101
11	Pelt	pan	----------111--	111101
14	Vite	sch	----------21---	111101
49	Swar	gra	----------11-1-	111101
52	MTN	17	------------2--	111101
54	Rino	bre	-------------2-	111101
55	Zoll	gra	-------------2-	111101
57	Alex	can	-------------2-	111101
6	Chom	bar	-1------2-2112-	11111
			000000000011111	
			000111111100001	
			0000011	
			01111	

Table 5.2. Twinspan two-way table based on the density data for trees ≥ 10 cm dbh from three different forest types on Maracá Island, Brazil. For the full names of the species see Appendix 2. In the columns for the fifteen plots '-' means that the species did not occur, and the values 1-5 refer to pseudospecies cut-level classes. Values in bold are non-preferential species.

			Plots	
Species			11111 1 134509278312456	
36	Dugu	luc	13122111------1	00000
21	Lica	kun	4232352111-----	000010
27	Pout	his	2321211111-----	000010
29	Guat	sch	2-111-11-1-----	000010
37	Ampe	ede	11-111-1-------	000010
38	Oura	cas	1--1111--------	000010
39	Bros	lac	2231-311-------	000010
26	Astr	acu	1222111--1-----	000011
41	Sloa	gar	1111----------	000011
48	Pinz	cor	-21----------	000011
28	Crep	gou	1122--2111-----	0001
30	Pout	ven	-111--111------	0001
33	Lind	pal	1121--111------	0001
31	Oeno	bac	1---1--1-------	00100
34	Tetr	pan	111233141------	00100
22	Pout	ret	1----31112-----	00101
23	Abut	gra	-----1---1-----	00101
24	Lueh	duc	------1-11-----	00101
25	Dryp	var	----2-12-1-----	00101
4	Lecy	cor	211215223512---	0011
9	Sima	ama	1-11-1113211---	0011
3	Eccl	gui	311144232511211	010
32	Amai	cor	--1111111-----1	010
12	Hima	art	111211311-2-1--	0110
17	Duro	eri	11112-111111--1	0110
19	Mach	sp	--1--111---1--1	0110
35	Ocot	fas	1-11--11----11-	0110
10	Maxi	mar	1-1-21315142---	0111
20	Coue	par	--------11---1-	0111
2	Prad	sur	2--122332224335	100
16	Euge	sp	-1-1------11---	100
46	Cord	sel	-11----------5	100
8	Pout	sur	121-1-111111211	101
13	Apei	sch	-111--111-1111-	101
14	Ente	sch	1---11----11---	101
1	Pelt	gra	-----1-22555555	110
7	Alse	lon	-111--12112231-	110
18	Euge	cup	----1--11--151-	110
40	Hyme	cou	1----------112	1110
47	Zygi	sp2	----------5	1110
15	Picr	cf.	-------1--12-11	11110
42	Zygi	sp1	----------211	11110
44	Case	ulm	----------131	11110
6	Chom	bar	--1-----1-2112-	111110
11	Pelt	pan	----------121--	111110
43	MTN	17	----------2--	111110
45	Rino	bre	----------2-	111110
5	Tabe	ule	----11----3411-	111111
			000000000011111 000011111100001 001111	

unidentified species (MTN 342) were the indicator species for the PRF6. Species that showed a continuous distribution are marked in Table 5.1. In general, the most abundant species (excluding *Peltogyne* and *Licania kunthiana*) were non-preferential species.

For trees ≥ 30 cm dbh, the most important indicator species for the first division were: *Brosimum lactescens, Licania kunthiana, Pouteria hispida,* and *Tetragastris panamensis* for the FWP group and only *Peltogyne* appeared as the main indicator species for the PRF plots. This last species occurred in all plots in this group with high abundance. Other species occurred in only a few plots of this group or with low abundance.

The TWINSPAN classification for the density data (Table 5.2), for both dbh classes, grouped the plots in exactly the same way as for the basal area data with also very similar divisions for species levels also. The removal of the two most abundant species (*Peltogyne* and *L. kunthiana*) from the matrix data showed exactly the same results for plot grouping with negligible differences for indicator species in both basal area and density data analyses.

FLORISTIC ORDINATION

PCA

The analysis for basal area data had eigenvalues of 0.522, 0.153, 0.069 and 0.058, respectively for the first four components produced. They accounted for 80% of the total variance.

The ordinations based on both basal area and density data for trees ≥30 cm dbh produced similar results to those found for trees ≥ 10 cm dbh. All the PCA's had some degree of distortion, reflected by the 'arch effect'. This fault was more pronounced for the density data analyses (Fig. 5.3b).

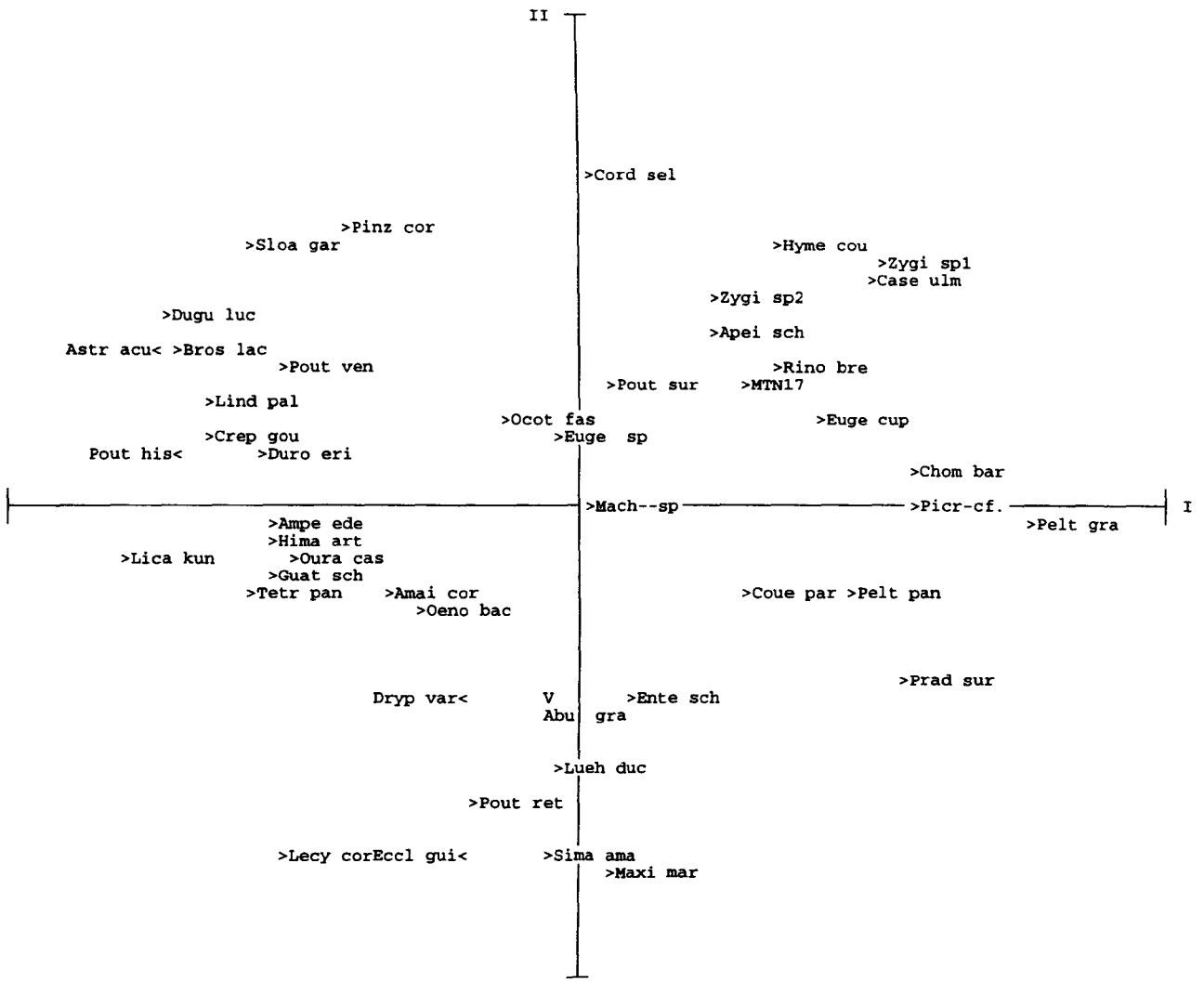


Fig. 5.3. (a) PCA ordinations of 48 most abundant species in the three forest types based on density data of trees ≥ 10 cm dbh. For the full names of species see appendix 2.

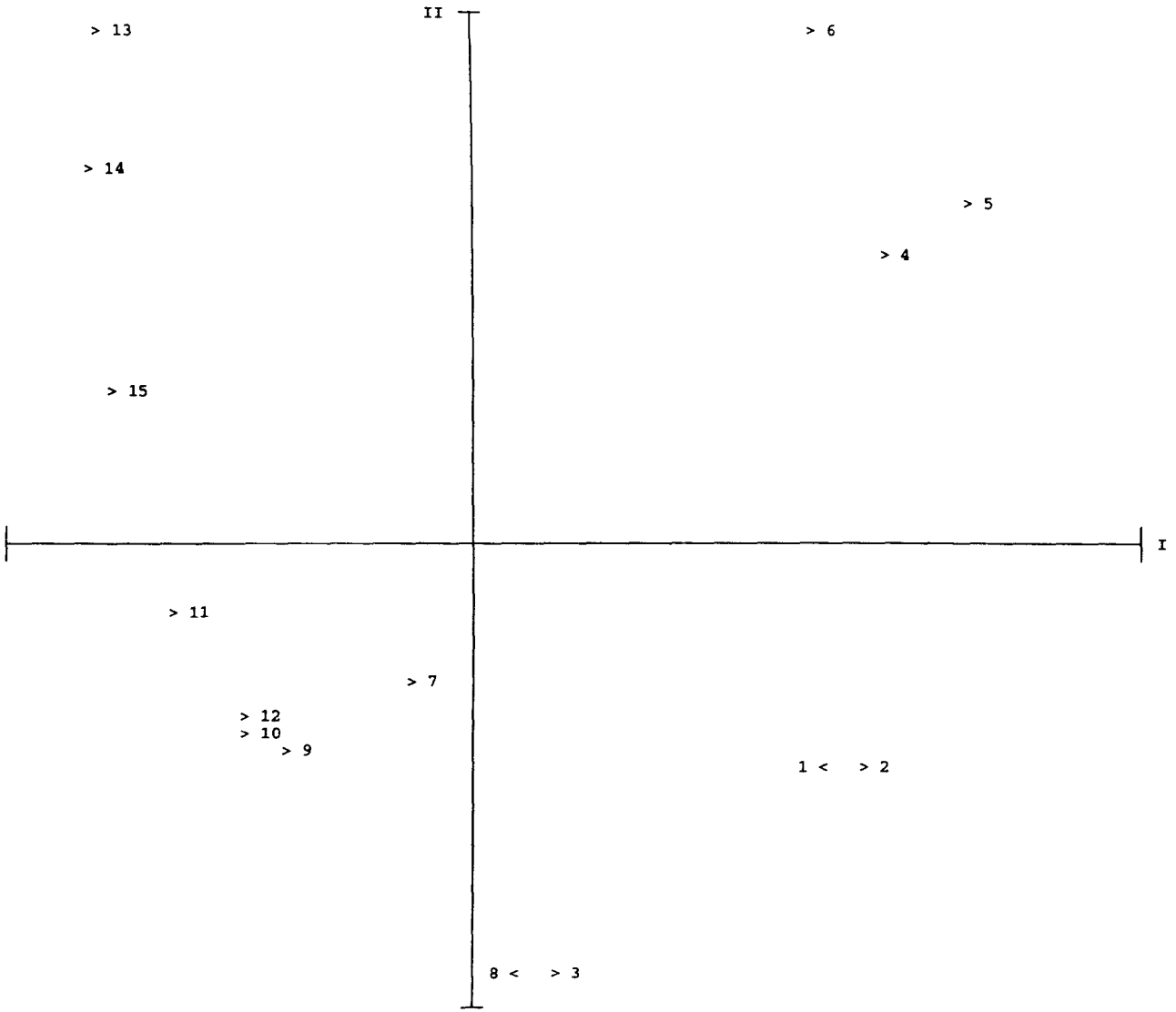


Fig. 5.3. (b) PCA ordinations of 15 Maracá forest plots based on density data of trees ≥ 10 cm dbh. Numbers 1-6, PRF; 7-9, PPF; 10-15, FWP.

DCA

Trees ≥ 10 cm dbh

The DCA ordination for basal area (Fig. 5.4) was similar to that for density data. In both analyses the eigenvalues for the first axis (0.61 for basal area data and 0.49 for density data) and the second axis (eigenvalue of 0.19 for basal area data and 0.18 for density data) were much higher than the eigenvalues for the third and fourth axes (all less than 0.06) which were considered unlikely to have much meaning. The most dominant species, *Licania kunthiana* and *Peltogyne* were placed at opposite extremes of axis I, whilst the other common species such as *Ecclinusa guianensis, Pradosia surinamensis* and *Simarouba amara* were plotted in the middle of the ordination of the corresponding species ordination.

Re-analyses of the basal area and density data, for trees ≥ 10 cm dbh, were made to check the effect of removing the two most dominant species, *P. gracilipes* and *L. kunthiana*. The results showed that for basal area data the eigenvalues changed mainly for components II and III, with their values being increased from 0.189 to 0.336 (axis II) and from 0.062 to 0.120 (axis III). The eigenvalues for the other two components (axes I, 0.680 and IV, 0.047) had their values slightly increased. This removal altered the position of the plot groups in relation to axes I and II. Comparing Fig. 5.4 with Fig. 5.5, it is clear that the plots from PRF were placed much more close to the plots from FWP. Excluding only *Peltogyne*, the values of the four eigenvalues (0.682, 0.336, 0.200 and 0.099) were similar to those found above, suggesting that *Peltogyne*, not *Licania*, caused most change. When *P. gracilipes* and *L. kunthiana* were excluded from the density data set the values of the eigenvalues were almost the same as those found in the former analysis. Neither the plot ordination nor the composition of the groups of plots changed much.

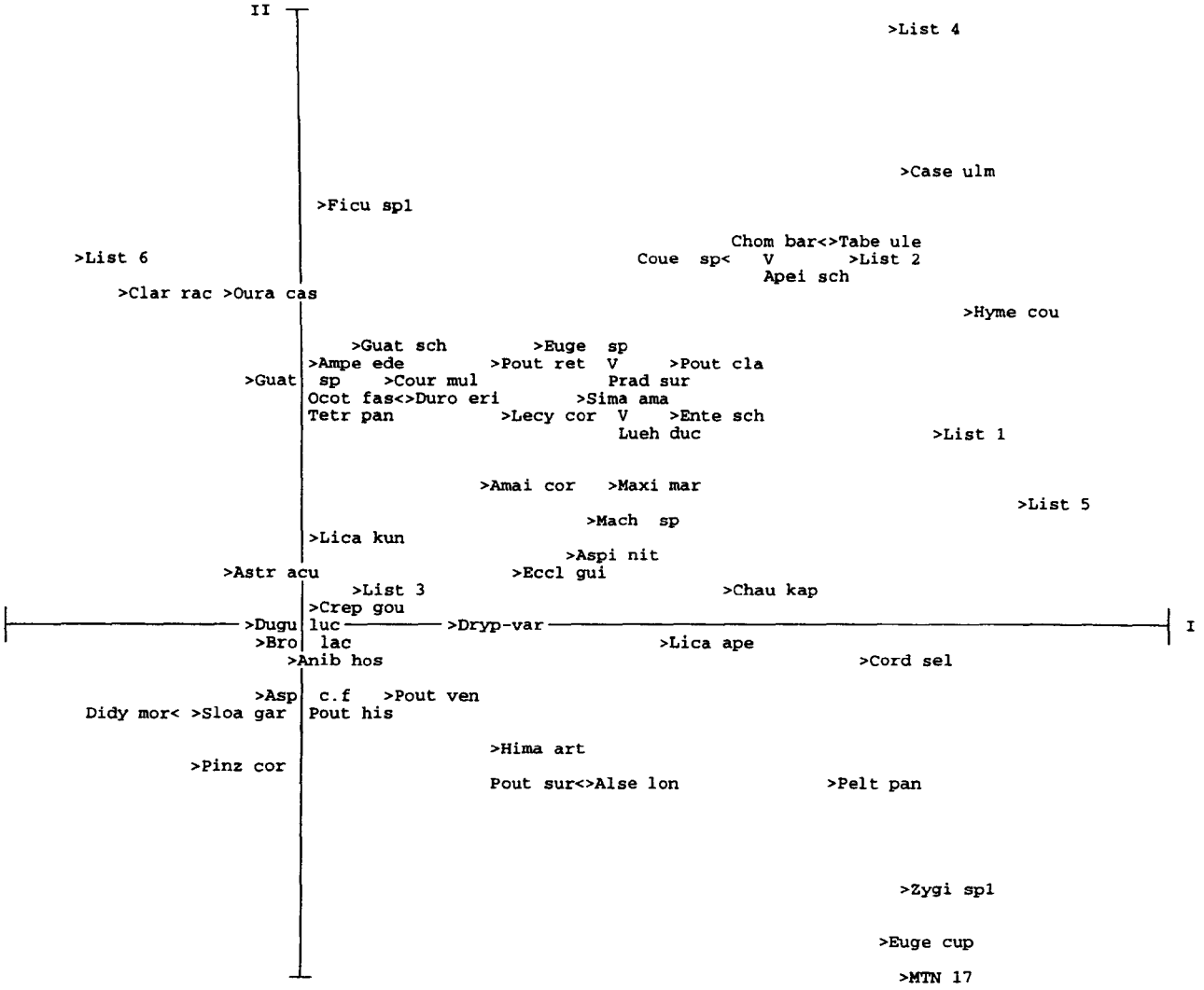


Fig. 5.4. (a) DCA ordinations of 66 most abundant species in three forest types on Maracá based on basal area data of trees ≥ 10 cm dbh. For the full names of the species see appendix 2. List 1= Pelt gra, Vite sch; List 2= Picr cf., Swar gra; List 3= Oeno bac, Lind par; List 4= Rino bre, Zoll gra, Alex can; List 5= Zygi sp2, MTN 342 and List 6= Swar dip, Pout ?, DS 628.

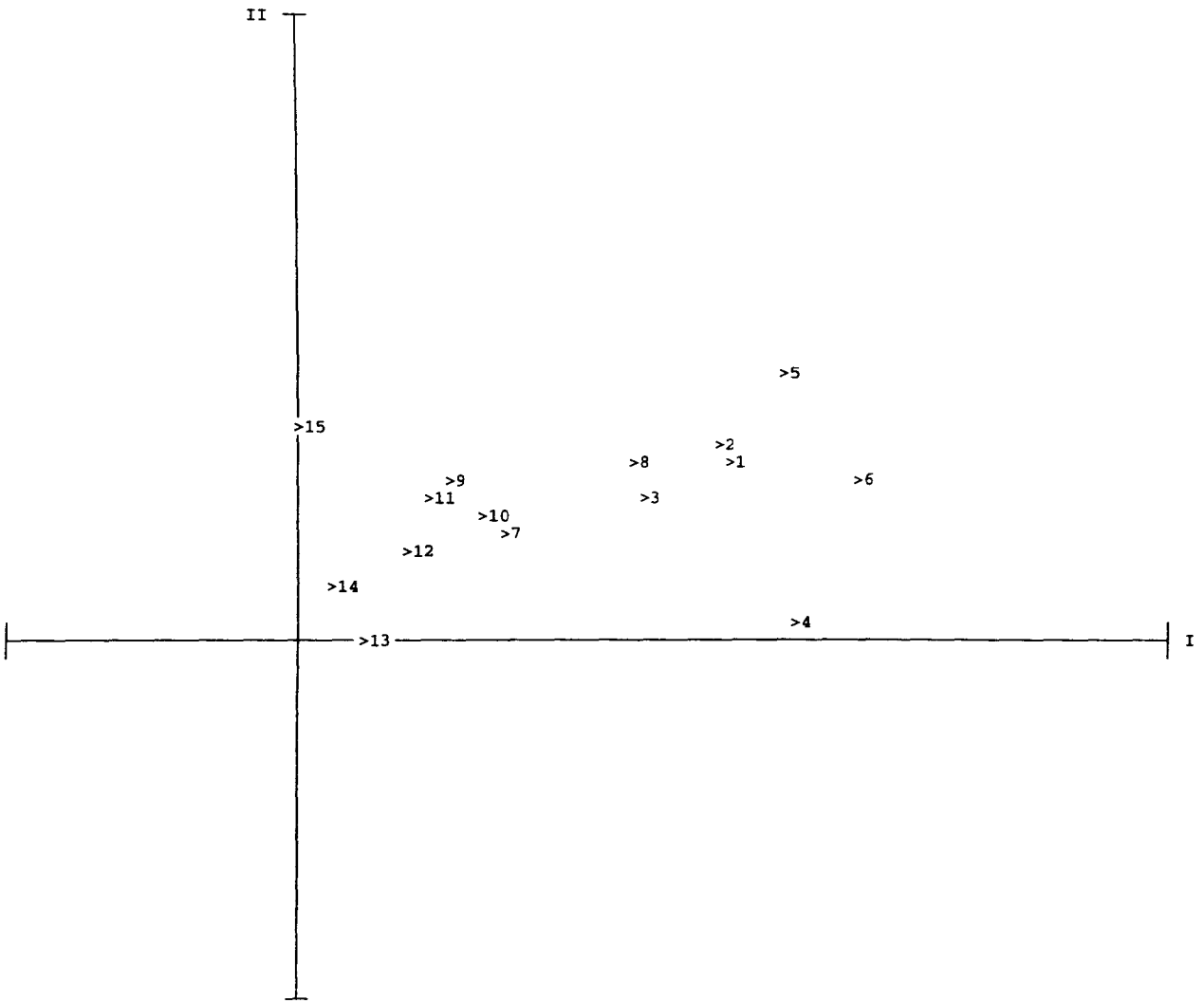


Fig. 5.4. (b) DCA ordinations of 15 forest plots on Maracá Island based on basal area data of trees ≥ 10 cm dbh. Numbers 1-6, PRF; 7-9, PPF and 10-15, FWP plots.

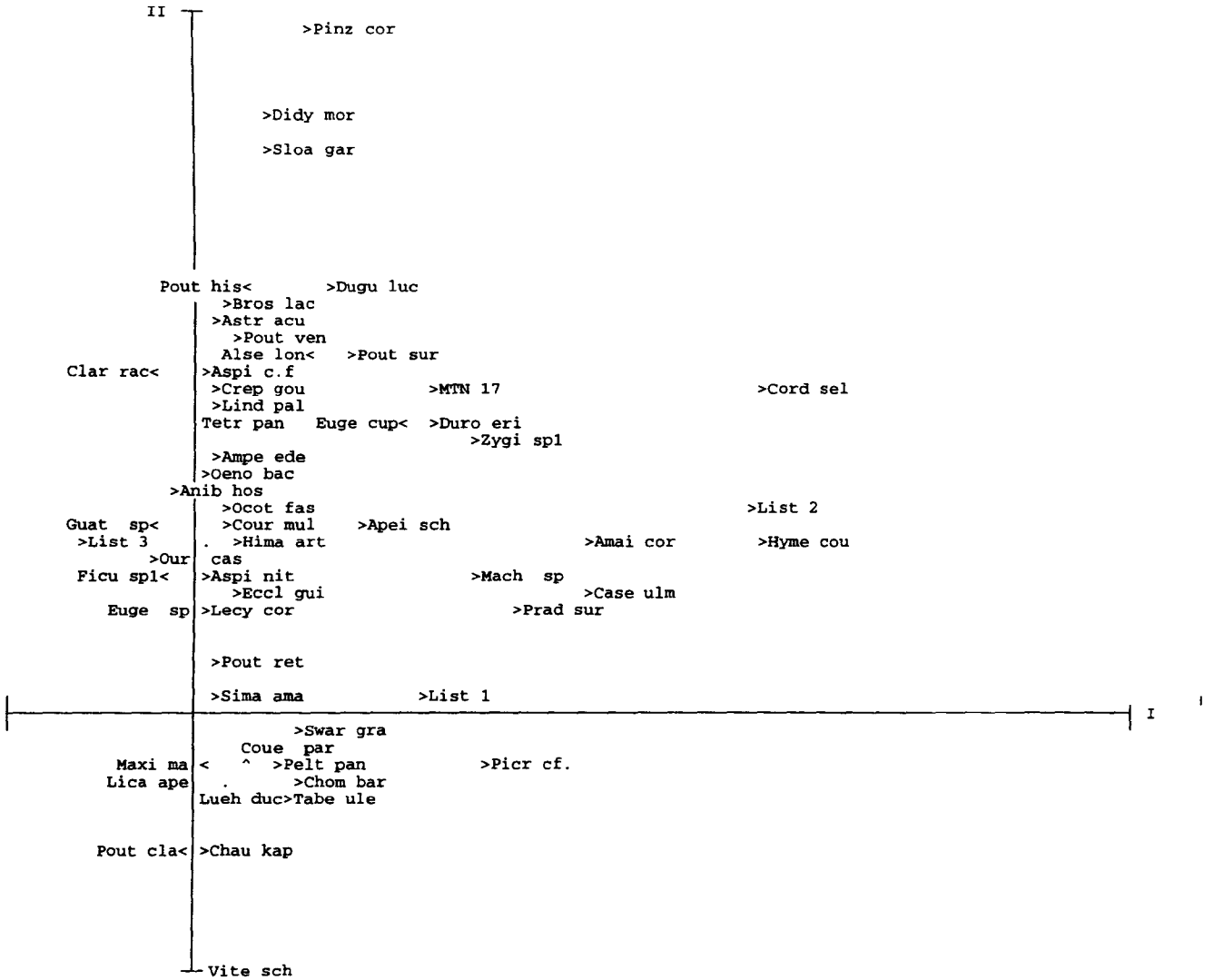


Fig. 5.5. (a) DCA ordinations of 64 most abundant species (excluding *P. gracilipes* and *L. kunthiana*) in three forest types on Maracá Island based on basal area data of trees ≥ 10 cm dbh. For the full list of species see Appendix 2. List 1= Rino bre, Zoll gra, Alex can; List 2= Zygi sp2, MTN 342; List 3= Swar dip, Pout ?, DS 628.

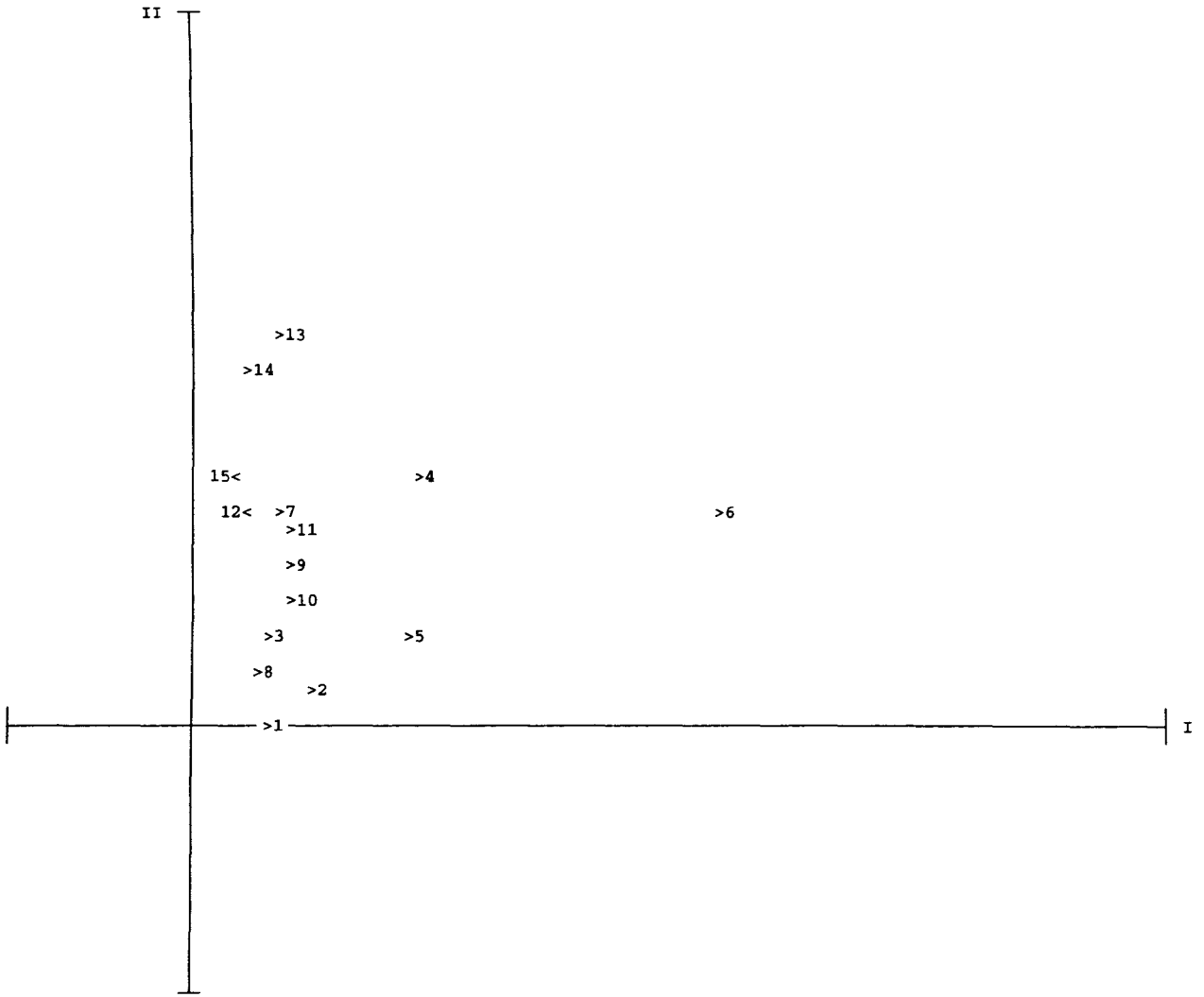


Fig. 5.5. (b) DCA ordinations of 15 plots in three forest types on Maracá Island based on basal area data of trees ≥ 10 cm dbh (excluding *P. gracilipes* and *L. kunthiana*). Numbers 1-6, PRF; 7-9, PPF; 10-15, FWP.

Trees ≥ 30 cm dbh

The ordinations of basal area and density data of trees ≥ 30 cm dbh were very similar to each other. These ordinations also produced similar results to those for trees ≥ 10 cm dbh.

VEGETATION-SOIL RELATIONSHIPS

PCA of the soil variables

The eigenvalues for the first four components were: 0.527, 0.244, 0.112, 0.046 (93% of the total variance). The first component of the analysis explained *c.* 50% of the total variance, with plots from FWP 10-12 and plots from PRF 4-6 separated at either end of axis I. Soil variables such as loss-on-ignition, silt, CEC and Mg were strongly positively correlated (r ≥ 0.82) with the first axis of the ordination and with plots from PRF. Sand (r= -0.91) was highly negatively correlated with this axis and so positively correlated with plots from FWP (Fig. 5.6). Soil variables such as P (r= 0.95), pH and Ca (both with r= 0.80) were positively correlated with axis II and so with FWP 10-12 plots, whilst the Mg/Ca quotient (r= -0.65) was the variable negatively correlated with this axis and highly associated with the plots from PPF and PRF (plots 1-3).

DCCA

Trees ≥ 10 cm dbh

The DCCA analyses for both the basal area and density data of trees ≥ 10 cm dbh gave similar results which were also similar to those produced by DCA for the plot and species ordinations (see Figs 5.4 and 5.7). The eigenvalues for the DCCA for the first two components were 0.565 and 0.222 (basal area data) and 0.467 and 0.057 (density data).

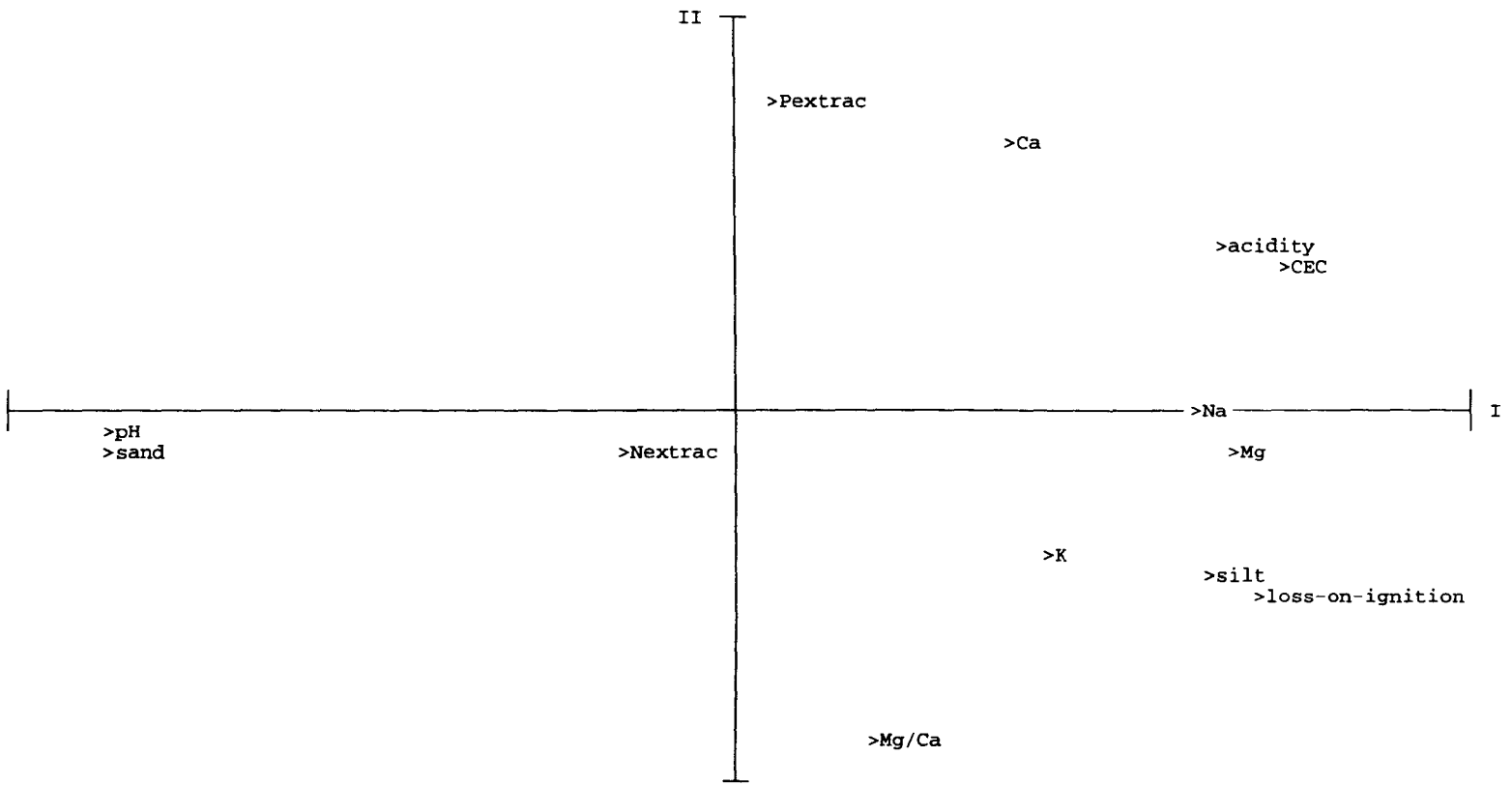


Fig. 5.6. (a) PCA ordinations of soil variables based on environmental data in the 15 plots.

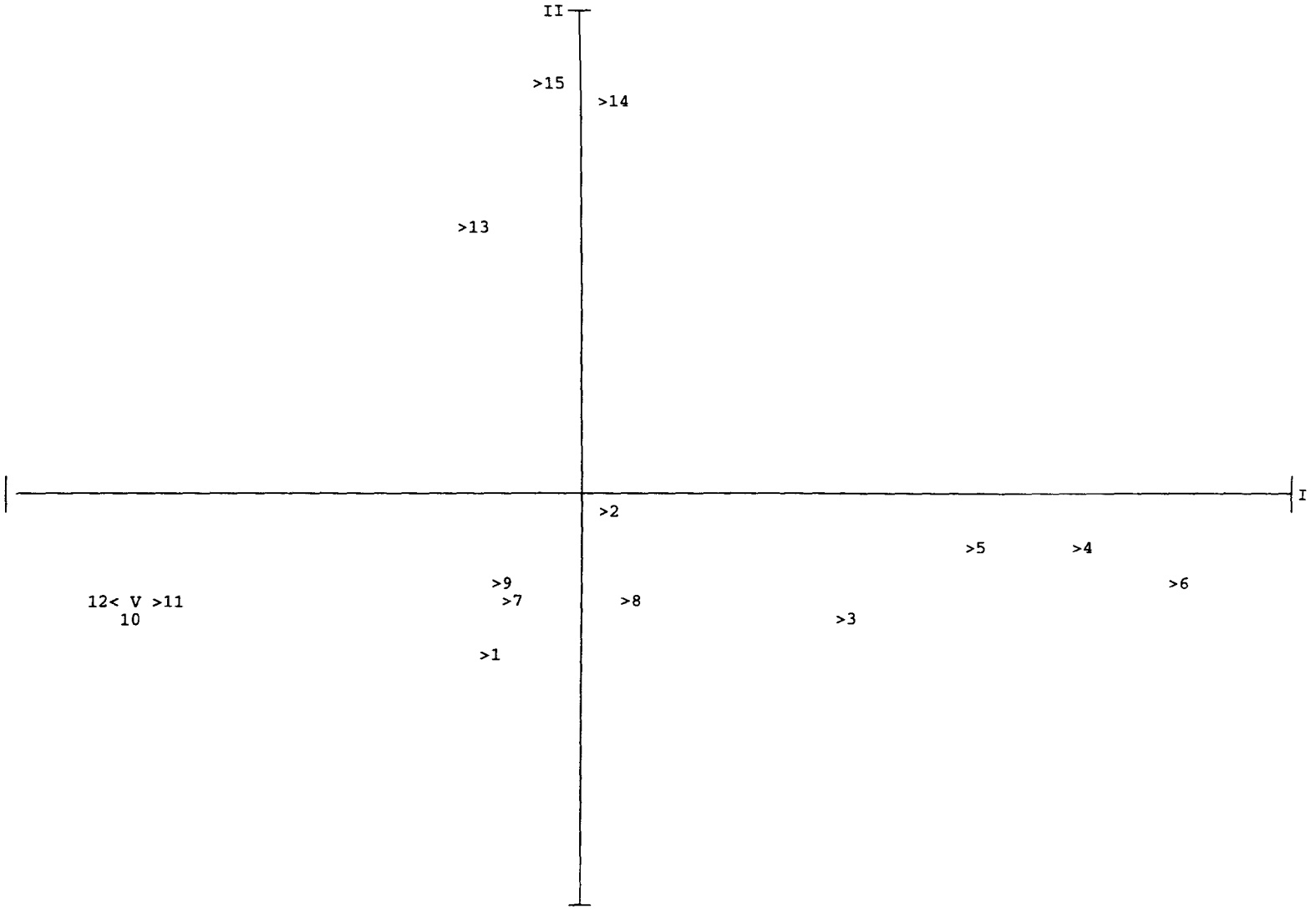


Fig. 5.6. (b) PCA ordinations of 15 plots based on environmental data. Numbers 1-6, PRF; 7-9, PPF and 10-15, FWP.

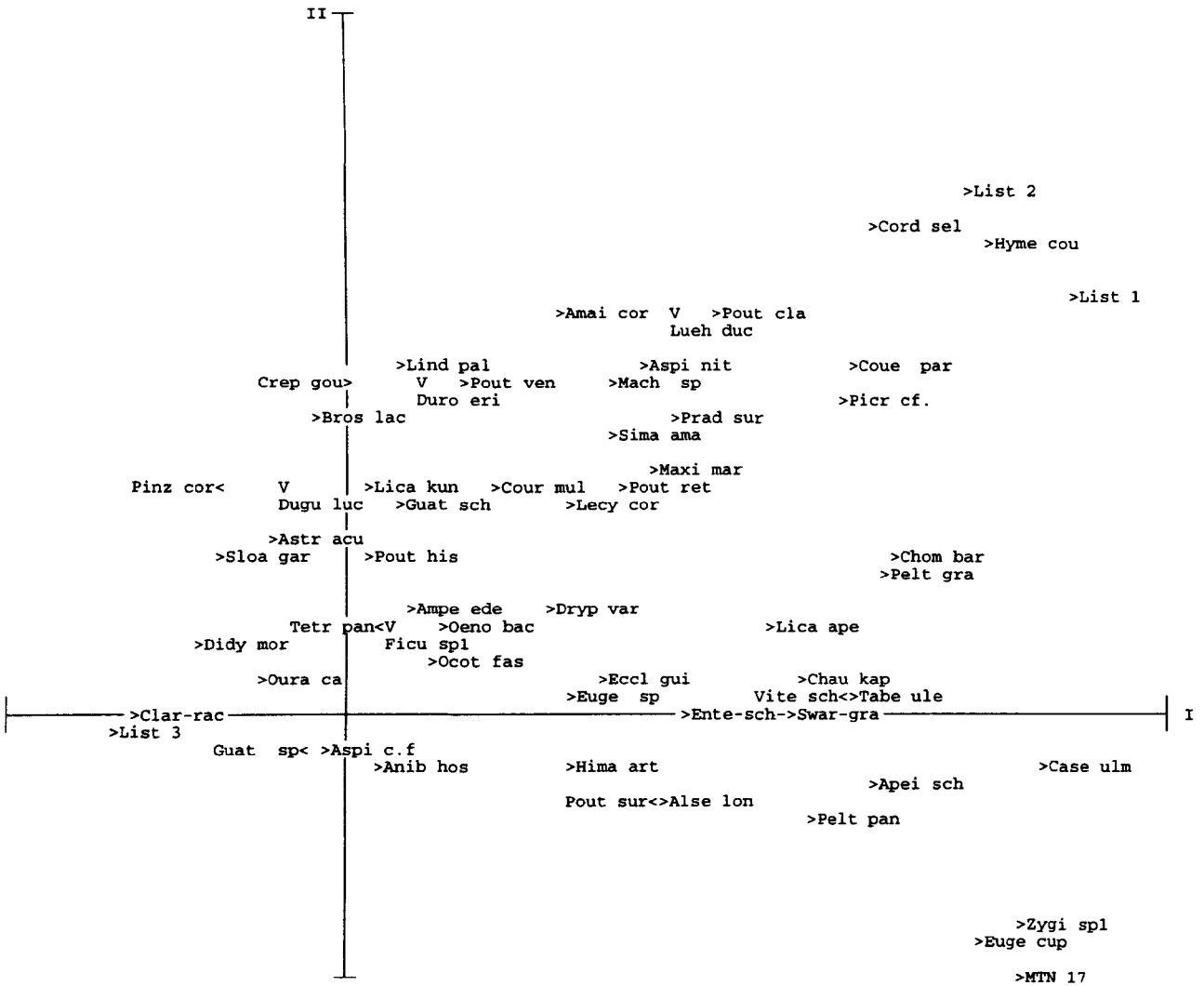


Fig. 5.7. (a) DCCA ordinations of the 66 most abundant species in the study plots based on basal area data for trees ≥ 10 cm dbh. For full names see Appendix 2. List 1= Rino bre, Zoll gra, Alex can; List 2= Zygi sp2, MTN 342; List 3= Swar dip, Pout ?, DS 628.

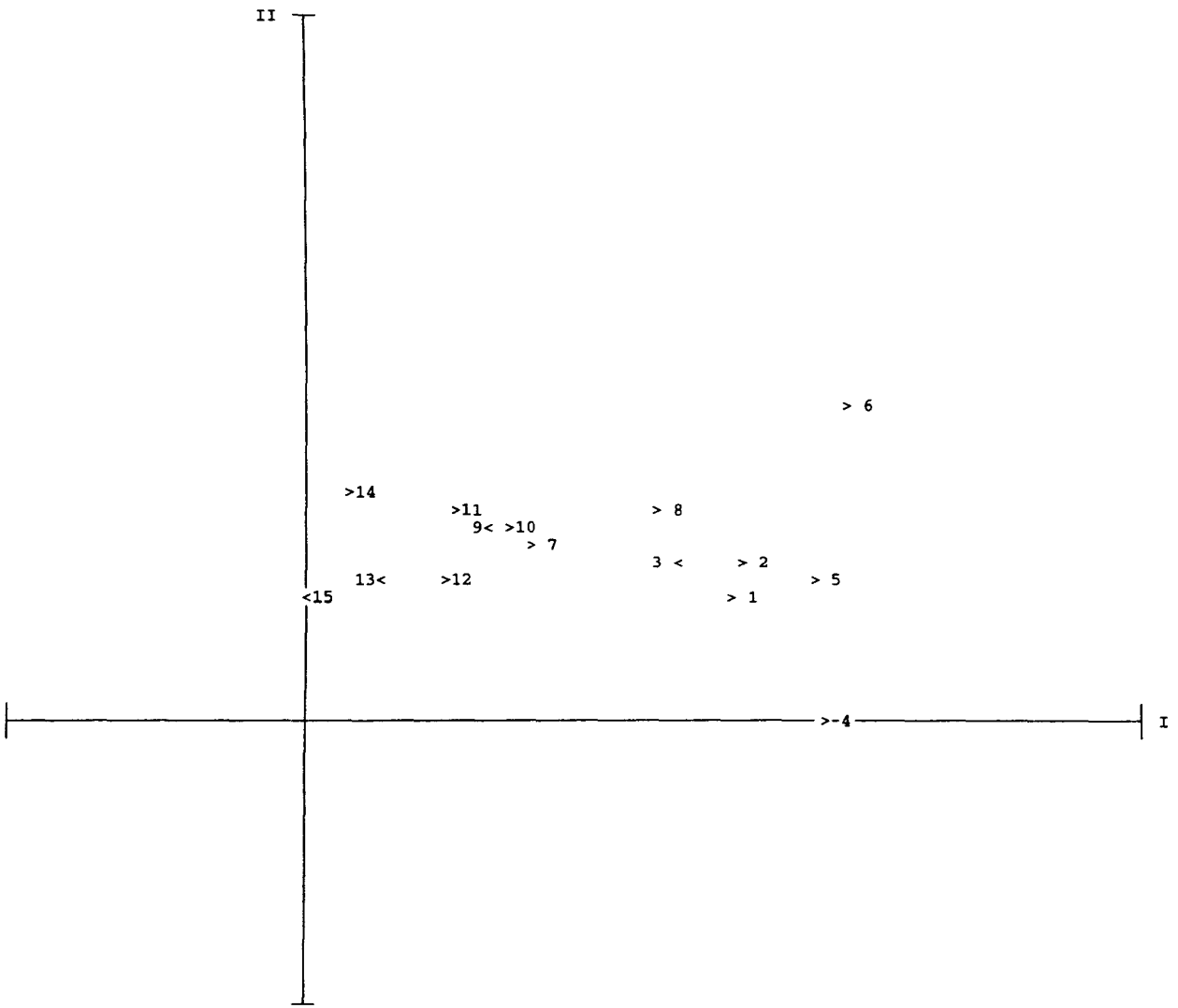


Fig. 5.7. (b) DCCA ordinations of 15 plots based on basal area data for tress ≥ 10 cm dbh.

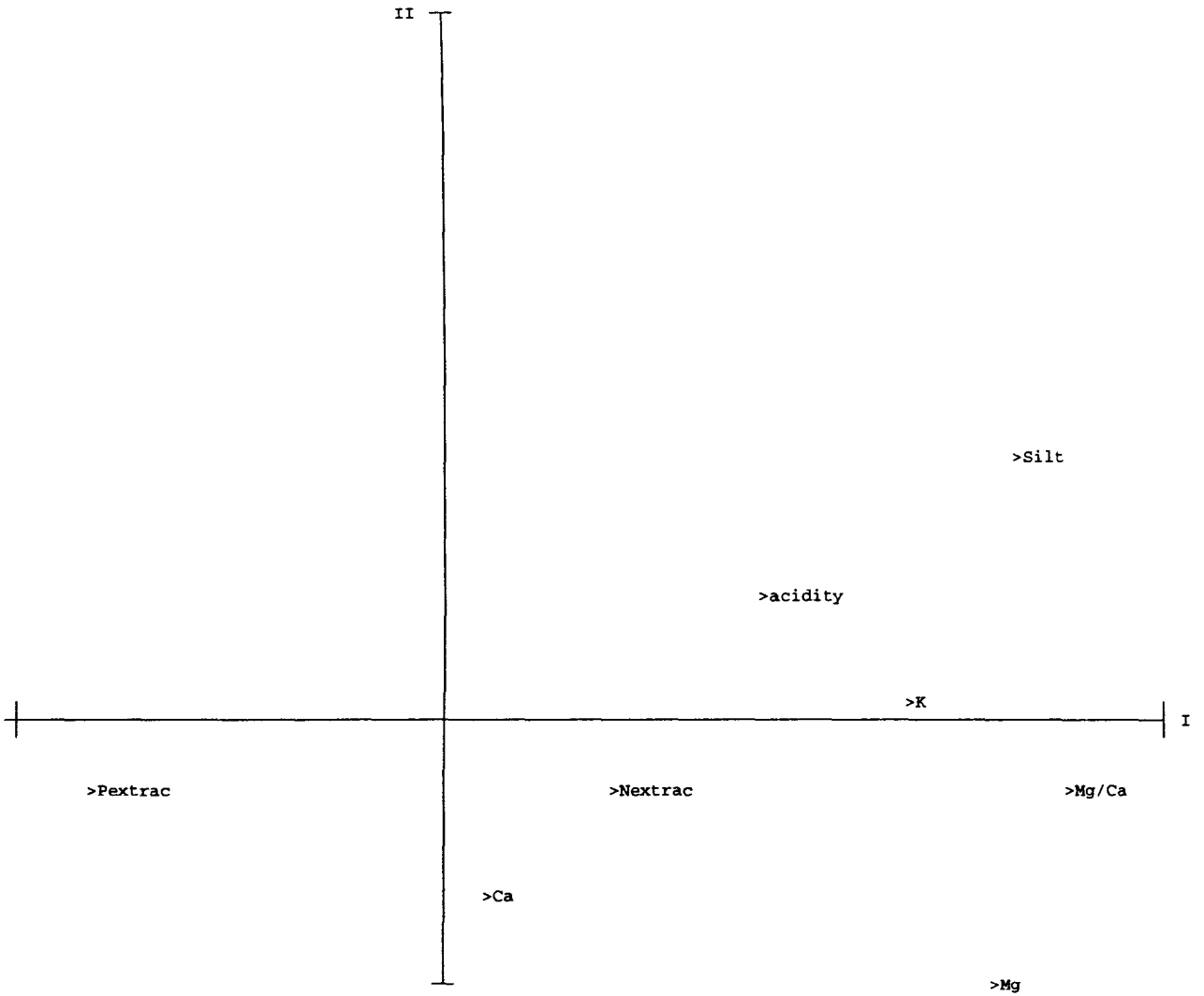


Fig. 5.7. (c) DCCA ordinations of environmental variables based on basal area data for tress ≥ 10 cm dbh.

The third and fourth axes had eigenvalues below 0.04. The cumulative percentage variance for species data for the first four components were 22.7%, 31.6%, 33.2% and 34.2%, respectively (basal area) and 27.8%, 31.2%, 32.1% and 32.8% (density). For species-soil relations the cumulative percentage variances were 29.7%, 39.3%, 39.3% and 39.3% (basal area) and 37.7%, 46.6%, 46.6% and 46.6% (density). The Monte Carlo test applied on the first canonical axis showed that the species were significantly related to the soil variables ($p \leq 0.01$) for both analyses.

Mg/Ca quotients (r= 0.86), Mg (r= 0.79), silt (r= 0.77) and K (r= 0.64) were positively correlated with axis I of the basal area data ordination, while P (r= -0.48) was negatively correlated (Table 5.3). The soil variables showed a weaker relation with axis II. Mg (r= -0.49) was the variable that showed the highest correlation coefficient with this axis (Table 5.3).

For the density data, the results were similar to those found for basal area data mainly for axis I. N (r= 0.66) and Ca (r= 0.53) were correlated with axis II.

The exclusion of *P. gracilipes* and *L. kunthiana* from the analyses yielded different results mainly for the basal area data principally in axes I and II of the ordination. These axes had their eigenvalues increased from 0.565 to 0.634 (axis I) and from 0.222 to 0.308 (axis II). Although the total cumulative variance of species data changed little (from 34.2% to 37.1%), the total cumulative variance of species-soil relationship decreased from 39.3% to 33.5% with the highest reduction occurring for axis I (from 29.7% to 17.4%). The reverse occurred for axis II, with an increase from 9.6% to 16.1% of the total cumulative variance of the species-soil relation. The removal of the two most dominant species decreased the correlation coefficients of Mg (from 0.79 to 0.32) and Mg/Ca quotient (from 0.86 to 0.31) and increased the values of silt (from 0.77 to 0.87) and acidity (from 0.44 to 0.68) with axis I. However, the negative correlation coefficients of Mg/Ca quotients increased (from

Table 5.3. Detrended canonical correspondence analysis (DCCA) of 15 plots in three forest types on Maracá Island, Brazil: matrix of weighted correlations (weighting factor= sample total for species' abundance and soil variables; soil variables standardised to zero mean and unit variance). Correlations in bold are significant at $p < 0.05$.

	Spp I	Spp II	Env I	Env II	N	P	K	Ca	Mg	Acidity	Silt	Mg/Ca
Spp axis I	1.000											
Spp axis II	-0.068	1.000										
Env axis I	**0.969**	-0.112	1.000									
Env axis II	-0.114	**0.950**	-0.118	1.000								
N	0.232	-0.111	0.239	-0.117	1.000							
P	-0.466	-0.047	-0.481	-0.049	0.237	1.000						
K	**0.625**	-0.045	**0.644**	-0.048	0.336	-0.025	1.000					
Ca	0.068	-0.252	0.070	-0.265	0.164	**0.692**	0.215	1.000				
Mg	**0.762**	-0.468	**0.786**	-0.493	0.170	0.009	**0.667**	**0.530**	1.000			
Acidity	0.428	0.133	0.442	0.140	0.004	0.241	0.344	0.397	**0.550**	1.000		
Silt	**0.748**	0.276	**0.772**	0.290	0.083	-0.191	0.485	0.240	**0.585**	**0.795**	1.000	
Mg/Ca	**0.837**	-0.195	**0.863**	-0.205	0.171	**-0.544**	**0.695**	-0.180	**0.676**	0.223	0.448	1.000

0.20 to 0.78) for axis II. After the removal of *L. kunthiana* and *Peltogyne* the soil variables showed a stronger correlation with axis II. Instead of only one variable (Mg), as found in the analysis without species exclusion, three variables (Mg/Ca quotient, r= -0.78; P, r= 0.77 and Ca, r= 0.64) were correlated with axis II. When only *Peltogyne* was excluded from the analysis the results were similar to those found in the analysis where both dominant species were removed, suggesting as found for DCA that the exclusion of *Peltogyne* affected more the results than the exclusion of *Licania*.

Trees ≥ 30 cm dbh

The ordination of plots and species in the first two axes by DCCA based on basal area and density data of trees ≥ 30 cm dbh showed small differences between each other. The eigenvalues for the first two axes were 0.638 and 0.211 (basal area data) and 0.586 and 0.196 (density data). In these analyses, the soil variables that showed strong correlation with axis I and II were essentially the same as those from the analyses of trees ≥ 10 cm dbh. However, it is noteworthy that Mg/Ca quotient had a very strong correlation with axis I (r= 0.92, basal area data and r= 0.88, density data).

Regression analysis

Among the ten most abundant species only three (*Licania kunthiana, Pouteria hispida* and *Peltogyne*) showed statistically significant ($P \leq 0.05$) relationships with some of the soil variables tested. For *L. kunthiana* four (P, K, Ca and Mg) soil variables showed a significant good fit, while *Peltogyne* correlated significantly with five (loss-on-ignition, K, Mg, clay and silt). *Pouteria hispida* had a significantly good fit for only two soil variables tested (Na, Ca). A summary of these results is shown in Table 5.4.

Table 5.4. Coefficient of determination (R^2) and significance level (p) of the regressions between species and soil variables. Only species that showed a significant fit ($P \leq 0.05$) to one or more soil variables are shown. LOI= loss-on-ignition, TA= total acidity. n= 15.
n.s= not significant; * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$. Values in bold were fitted by linear model, others by cubic terms of a polynomial function.

	LOI	P	K	Na	Ca	Mg	TA	clay	silt
L. kunthiana	0.48 n.s.	0.51 *	0.64 **	0.15 n.s.	0.52 *	0.59 *	0.21 n.s.	0.48 n.s.	0.34 n.s.
P. gracilipes	0.81 ***	0.55 n.s.	0.57 *	0.37 n.s.	0.46 n.s.	**0.73** **	**0.22** n.s.	0.62 **	0.72 **
P. hispida	0.37 n.s.	0.11 n.s.	0.14 n.s.	0.64 **	0.65 **	**0.12** n.s.	0.29 n.s.	**0.11** n.s.	**0.12** n.s.

It is important to highlight that the soil variables that showed the highest coefficients were loss-on-ignition (R^2= 0.81) and Mg (R^2= 0.73) for *Peltogyne* and Mg (R^2= 0.59) for *L. kunthiana* (Fig. 5.8).

DISCUSSION

FLORISTIC CLASSIFICATION AND ORDINATION

The classifications using both TWINSPAN and cluster analysis (UPGMA) methods led to similar conclusions. Two major groups were defined: 1) plots from PRF and 2) plots from FWP, with the PPF plots being more associated with FWP.

An advantage of using TWINSPAN instead of cluster analysis is that the former method integrates the classification of both samples and species and so produces an arranged data matrix (Gauch 1982). Recently some authors have re-evaluated the TWINSPAN method (van Groenewoud 1992 and Belbin & McDonald 1993) and found that this method fails when the two gradients have the same length, but this was not the case here. Belbin & McDonald (1993) compared TWINSPAN and a flexible variant of UPGMA and concluded that UPGMA was significantly better than TWINSPAN, mainly because TWINSPAN showed two problems: dependence on a predominant primary gradient and dichotomising at an inappropriate point on this axis. However, in this study both methods split the groups in a similar way.

The list of the indicator and non-preferential species for the groups of plots yielded by TWINSPAN showed that the two most dominant species, *Peltogyne* (group 1) and *L. kunthiana* (group 2) were good indicators for those groups and suggested that their relationships with some environmental variables could explain, at least in part, the pattern observed. Species that occurred in all three forest

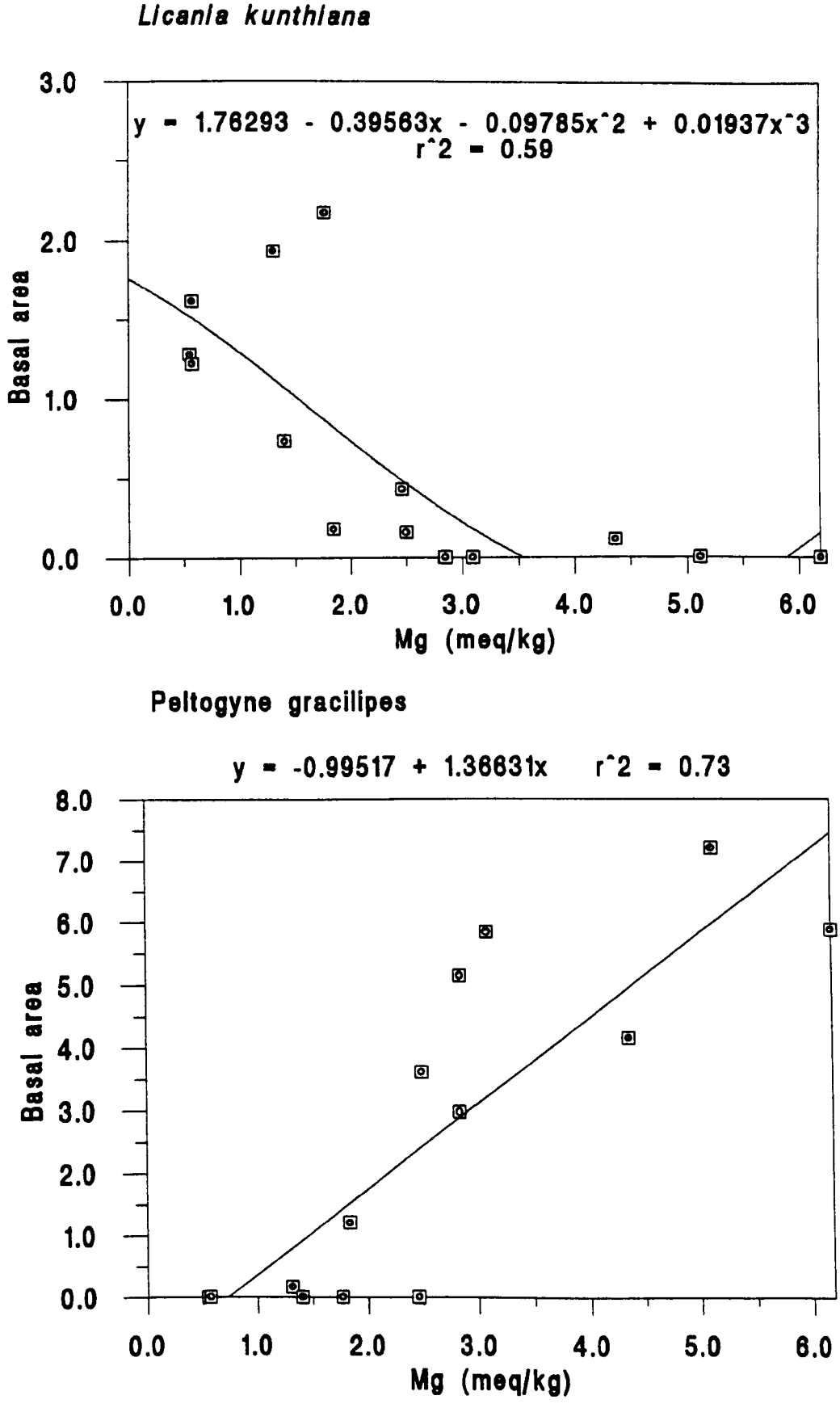


Figure 5.8. Relationship between Mg concentration in soil surface and basal area of trees (≥ 10 cm dbh) for *Licania kunthiana* and *Peltogyne gracilipes*.

types (non-preferential) such as *Ecclinusa guianensis*, *Lecythis corrugata*, *Maximiliana maripa*, *Pradosia surinamensis* and *Simarouba amara* were reported by Milliken & Ratter (1989) as widespread in Maracá forests. The fact that the forest types were subjectively chosen according to the number of *Peltogyne* trees suggests that the results of the classifications might be interpreted as circular. However, the classification analyses showed that instead of three different forest types two major groups were recognised, with plots from PPF placed together with plots from FWP. Another important point was that the removal of *L. kunthiana* and *Peltogyne* from the TWINSPAN analyses did not produce different results. Therefore, the classification of the forest could not be explained as a result of the dominance of those species and showed that other species were associated.

The different methods of ordination (PCA, DCA and DCCA) produced similar results and only a slight difference was found between analyses based on basal area or density data. Newbery (1991) found similar results, at the group and subgroup levels, when both CA and PCA were applied on floristic data from heath forests in Sarawak and Brunei. He highlighted that a CA does not weight higher abundances accordingly. However, for the Maracá data the PCA technique showed the arch effect in all analyses. This fault has been reported by several authors (see Gauch 1982, Greig-Smith 1983, ter Braak 1987, Kent & Coker 1992) as one of the main problems in using the PCA or CA and when it occurs a DCA analysis is recommended. Thus, although the PCA results for plot group composition did not differ too much from the DCA results they were not considered here because of the arch effect.

The two most abundant species, *Peltogyne* and *L. kunthiana* had a high positive (*Peltogyne*) and negative (*L. kunthiana*) correlation with axis I of the DCA and DCCA ordinations. Those species, in general, reach large dimensions and occur with a high number of individuals in

PRF (*Peltogyne*) and FWP (*L. kunthiana*). As found for the TWINSPAN classification, the removal of those species from the basal area and density data set showed that only the analyses based on basal area data changed the results for plot ordination. Thus, the basal area of these two species, but specially *Peltogyne*, appears to play a more important role than their density in the ordination. Gartlan *et al.* (1986) also found that the plots from Korup forest in Cameroun were mainly ordinated along the gradient according to the abundance of the two most dominant species, *Oubanguia alata* and *Scyphocephalium mani*. These species differed in their type of size-class distribution, with *O. alata* having mostly small (10-20 cm dbh) trees and very few individuals greater than 50 cm dbh, while *S. manii* showed the reverse. *Peltogyne* and *Licania kunthiana*, on the other hand, had the same type of size-class distribution.

Plots from PPF were classified and ordinated in the same group as FWP plots, except plot PPF8 which was, in most analyses, placed together with PRF3 in a separate group. The ordination analyses also showed plots from FWPb and PRFb placed at each extreme of the diagram. This is in agreement with the location of the plots in the field, since plots PPF 7 and PPF 9 were more distant from PRF, and FWPb and PRFb were located far from each other with plots from FWPa and PRFa between them. Thus, these results suggest that despite the similarity within forest types, the position of FWPb and PRFb plots on the Island reflected the floristic differences. Milliken & Ratter (1989) showed that the floristic composition of Maracá forests changes gradually from the eastern to western part of Maracá.

SPECIES-SOIL RELATIONSHIPS

The negligible differences found between DCA and DCCA analyses, with plots and species placed in the same areas of the diagrams, suggested that the soil and species axes were

highly related with *c.* 40% of the total variance explained. Therefore, the soil variables supplied in this study could explain only partially the floristic variation among plots. However, according to ter Braak (1988) lower values for percentage variance are normally found and do not make the relations less meaningful.

Soil variables such as Mg and silt defined the first axis ordination, in both PCA and DCCA analyses. These results strengthened the suggestion in Chapter 4 that Mg should be one of the most important variables related to the floristic differences amongst forest types.

The regression analyses showed that *Peltogyne* had a positive correlation with Mg concentrations, while *L. kunthiana*, the most abundant species in FWP, had a negative one. The other dominant species such as *Ecclinusa guianensis*, *Lecythis corrugata*, *Pradosia surinamensis* and *Tetragastris panamensis* did not show any relation with Mg. Thus, the fact that PRF has more Mg in the soil than FWP could be explained simply by considering it a result of the effect of the magnesium-rich *Peltogyne* litter. *Peltogyne* has high concentrations of Mg in its leaves, fruits, flowers and wood (D. Villela, personal communication). However, the highest concentrations of Mg and the highest Mg/Ca quotients occurred in the deepest soil horizon (≥ 80 cm from the surface) (Table 4.1, Chapter 4). Several authors have shown that Mg and Ca are easily released from the litter through decomposition process (Chuyong 1994, Luizão *et al.* 1995). Leaching of Mg from the surface and its accumulation at depth could be a possible explanation for the highest concentration of Mg in the deepest soil horizon. In view of the lack of known mechanism of magnesium accumulation it is just as or more likely that the high soil magnesium concentrations reflect a difference in parent material.

Mg has also been reported to be strongly correlated with species distributions in mixed dipterocarp forest in central Sarawak, Malaysia (Baillie *et al.* 1987) and in Tabonuco forest in Puerto Rico (Johnston 1992). Ashton

(1989) found that, in a dipterocarp forest in Borneo, the species-richness was positively correlated with soil magnesium when the "reserve" (concentrated hydrochloric acid extractable) Mg concentration was below 1200 $\mu g\ g^{-1}$, but above it was negatively correlated. The biological explanation for this is not easy, however according to Baillie *et al.* (1987) Mg availability may affect the efficiency of mycorrhizal root systems and so could reflect different degrees of dependence on this nutrient in the mycorrhizal systems for efficient P uptake from soils that are poor in available phosphorus. In the case of Maracá forests, this assumption seems not be appropriate since PRF and FWP did not differ in P availability and the most abundant species in PRF (*Peltogyne*) and in FWP (*L. kunthiana*) seem to have vesicular-arbuscular mycorrhizal (VAM) associations (see Chapter 11 for more details). While there is some justification for the analyses of "reserve" magnesium made by Ashton and others, the technique has rarely been used outside Borneo and makes detailed comparisons with other studies impossible.

CONCLUSION

The multivariate analyses applied here showed that the two most dominant species in Maracá forests are strongly positively (*P. gracilipes*) and negatively (*L. kunthiana*) correlated with some soil variables, especially Mg, Mg/Ca, clay and silt. However, as pointed out by Newbery & Proctor (1984) correlative evidence is insufficient to prove causality and experimental studies are required. Thus, one approach might be through fertilization experiments, using different concentrations of Mg in soils from FWP with a range of species including the two dominants.

Chapter 6. Population dynamics of five non-pioneer trees in three forest types on Maracá Island.

INTRODUCTION

The species composition and structure of tropical rain forests has been considered to be related to gap formation (e.g. Connell 1978, Hartshorn 1980, Whitmore 1984, Brokaw 1985, Denslow 1987), with the role of canopy gaps as sites of successful tree regeneration in closed forests widely recognized by forest ecologists. However, as pointed out by Proctor (1991) demonstrations of this are rare with few data available on microsite and growth. Recently Clark & Clark (1992) studied the life history of six non-pioneers in a primary forest at La Selva, Costa Rica and concluded that the simple concepts of tolerance and gap dependence for tropical wet forest need to be reevaluated or even abandoned because of the complexity in species' life histories. Nevertheless, the diversity of trees in rain forests depends on the successful recruitment of seedlings, saplings and small trees into the canopy. Clark & Clark (1987) pointed out the lack of studies which cover all size classes of a species from seedling to adult.

This chapter will deal with the natural regeneration of five non-pioneer tree species occurring in PRFa, PPF and FWPa. In addition a brief comparison of the growth and mortality rates of seedlings of two species (*Peltogyne* and *Pradosia surinamensis*) in a small natural gap and under the closed canopy will be provided.

This Chapter reports an analysis of the relationship between the abundance of adult trees, especially *Peltogyne*, and their smaller size-classes and an attempt to classify the *Peltogyne*-rich forest into one of the two mono-dominant forest categories proposed by Connell & Lowman (1989): 1) rain forests with a persistent dominant and 2) rain forests with a non-persistent dominant.

METHODS

SPECIES SELECTION

Five tree species which had a large number of individuals (≥10 cm dbh) in at least one of the three study forest types were selected. The selected species were: *Ecclinusa guianensis, Lecythis corrugata, Licania kunthiana, Peltogyne and Pradosia surinamensis*. All these are non-pioneers according to Swaine & Whitmore's (1988) classification. Henceforth in this Chapter all the species will be referred to by their generic names only.

PLOT SAMPLES

All individuals (≥10 cm dbh) of the selected species in the three 50 m x 50 m replicate plots in each of PRFa, PPF, and FWPa were recorded, measured for the girth at breast height (1.3 m) (gbh), and marked on 1-14 October 1991, with a permanent aluminium tag. Tree mortality was checked on 21-22 March 1994 in the PRFa and FWPa plots. In PPF only one (PPF9) of the three plots was checked because of lack of time, and its result (one dead tree was found) will not be considered because of the small sample.

Seedlings (≤50 cm tall) and saplings (>50 cm tall, <10 cm dbh) of the selected species were sampled in five sub-plots of 2 m x 1 m (seedlings) or 4 m x 4 m (saplings) placed in a stratified random manner within each plot. The initial sampling, for both categories, was carried out on 18-24 October 1991 and all the seedlings and saplings from the five study species in each quadrat were labelled with an aluminium tag. Further censuses were made on the following dates: 20-22 April 1992, 22-24 July 1992 (seedlings only), 15-17 March 1993, and 13-16 March 1994 (seedlings only). At each census the height or the gbh or both of each tagged

plant was recorded and the new recruits tagged. Height only was measured for individuals ≤ 2 cm gbh. Height was defined as the vertical distance from the stem base to the highest live meristem. The number of leaves (old and new) was counted only for individuals smaller than 2 cm gbh.

GAP SAMPLES

In July 1991, a fallen tree created a medium gap (33 m long and 12 m wide), near plot PRF2. Thirty individuals (≤ 50 cm tall) of each species, *Peltogyne* and *Pradosia*, were tagged and measured, as described above, in August 1991. Remeasurements were made in February 1992, August 1992 and March 1993).

For all individuals (trees, saplings and seedlings) which were clearly dead the possible cause of death was recorded. In cases of doubt (e.g., leafless but with a solid stem), the individual was recorded as alive but if it was not alive at the next visit, the previous census was noted as the time of the death.

DATA ANALYSIS

Plant mortality

The mortality rates of the cohort of individuals (with a range of unknown ages) first measured in October 1991 (recruits were not included) in each forest type were calculated by the log model annual mortality rate (EAMR) (Swaine & Lieberman 1987): $EAMR = 100(\log_e n_0 - \log_e n_1)/t)$, where n_0 is the number of individuals at the first measurement; n_1 is the number surviving at the second enumeration, after t years. According to Swaine & Lieberman (1987) this model is better than the arithmetical version ($m=100(n_0-n_1)/t$) because it implies that the proportion of

survivors dying in each time interval is constant, not increasing, and dependent on the interval, t, between censuses. The population half-life ($t_{0.5}$) was defined as the number of years for the initial population to fall to 50%: $t_{0.5}$= ($\log_e$ (0.5))/(0.01EARM) (Swaine & Lieberman 1987).

For the statistical analysis a Chi-square test with the significance level set to 0.05 was carried out. The two-tailed Fischer's exact test was used when more than 20% of the expected frequencies were less than 5.0 (Zar 1984).

Growth rates

Annual height and girth growth of each study species were assessed as the difference between two measurements divided by the number of days between the two censuses, all multiplied by 365. As for mortality rates, the growth rates were calculated using only the survivors of the entire period. A Kruskal-Wallis non-parametric ANOVA was carried out to compare the growth rates among species, with the significance level set to 0.05. When there were ties in the data they were adjusted (Zar 1984). A multiple pair-wise Mann-Whitney U two-sample test was used for multiple comparisons when a significant result was obtained by the ANOVA. According to Day & Quinn (1989) non-parametric tests for unplanned multiple comparisons have an inflated risk of Type I errors. However, following Clark & Clark (1992), the interpretation of pair-wise tests was done only in cases where $P \leq 0.01$. Where a species had less than five individuals it was not considered in the analysis. Individuals with zero or negative net growth rate are referred to as 'suppressed'.

RESULTS

POPULATION STRUCTURE OF THE SPECIES

The population structures of each studied species in the three forest types are shown in Figures 6.1 to 6.3. Most of the species had a similar pattern among forests, with about 90% of the individuals being seedlings and less than 1% trees. However, *Lecythis* and *Licania* did not show this pattern in PRFa, with *Lecythis* occurring only as trees (25%) and saplings (75%), while *Licania* had only trees (100%).

It is important to highlight that the values of absolute density of *Ecclinusa*, *Lecythis* and *Licania* were much higher in FWPa and PPF than in PRFa, mainly for saplings and seedlings (Table 6.1).

SIZE DISTRIBUTION OF TREES

The distribution of diameters (≥ 10 cm dbh) of all trees (Fig. 6.4) and of the five tree species in each forest type (Fig. 6.5) showed that most of the individuals were distributed within the small tree class (≥ 10 cm-≤ 30 cm dbh) with a reversed-J shape in all of the cases.

It is noteworthy that in PRFa only *Peltogyne*, among the five selected species, occurred as large trees (≥ 50 cm dbh). For each species, the maximum dbh in PRFa was 30.4 cm (*Licania*), 38.6 cm (*Ecclinusa*), 39.2 cm (*Lecythis*), 47.4 cm (*Pradosia*), and 143.2 cm (*Peltogyne*). In PPF most of *Peltogyne* trees (50%) were more than 50 cm dbh (maximum of 132.6 cm). The other species occurred in this forest mainly as small trees but showed an increase in the number of large trees. The highest number of large trees of the selected species were found in FWPa with the maximum dbh of 49.3 cm (*Ecclinusa*), 54.2 cm (*Lecythis*), 76.4 cm (*Licania*), and 77.6 cm (*Pradosia*).

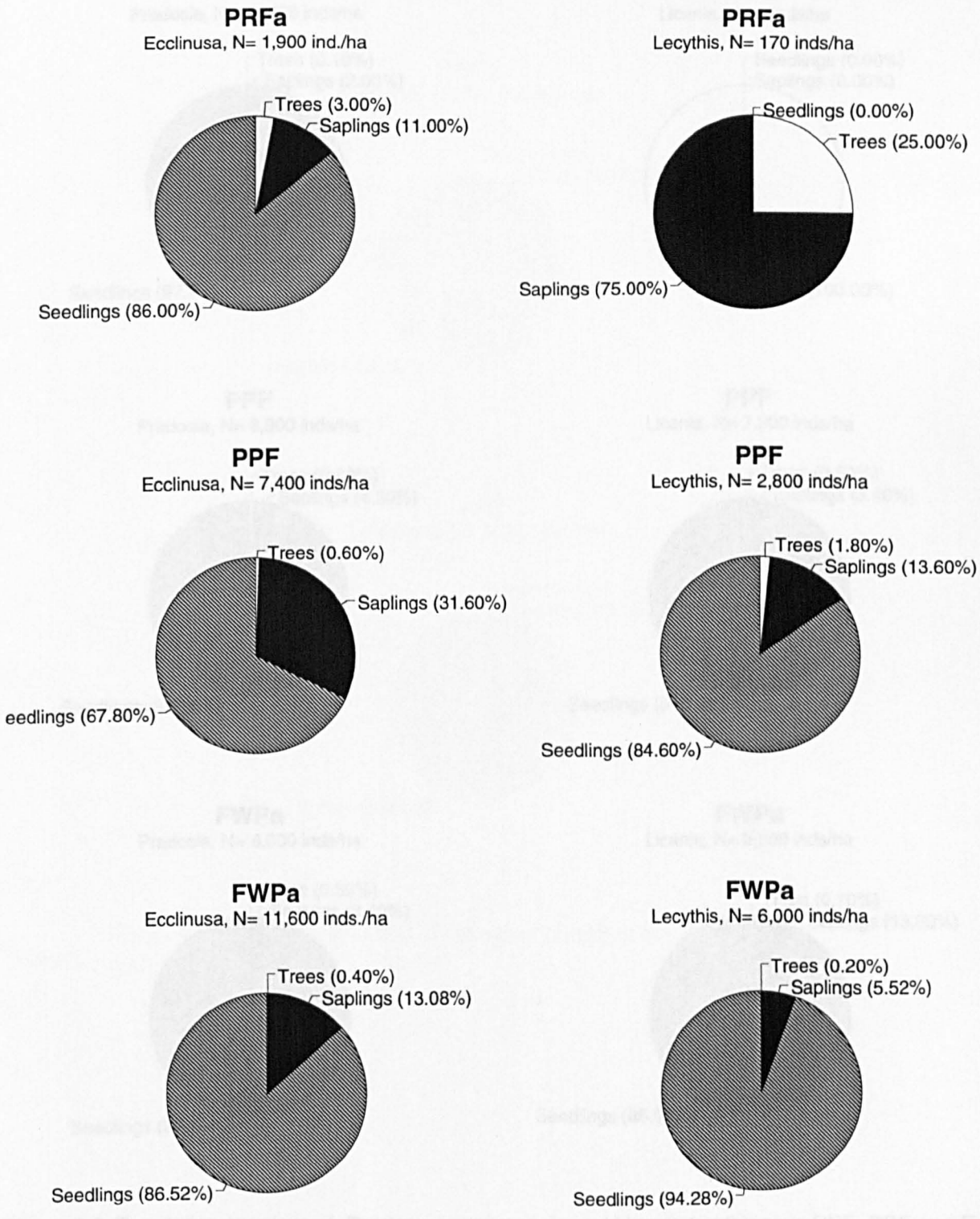


Figure 6.1. Population structure of Ecclinusa guianensis and Lecythis corrugata in PRF, PPF and FWP.

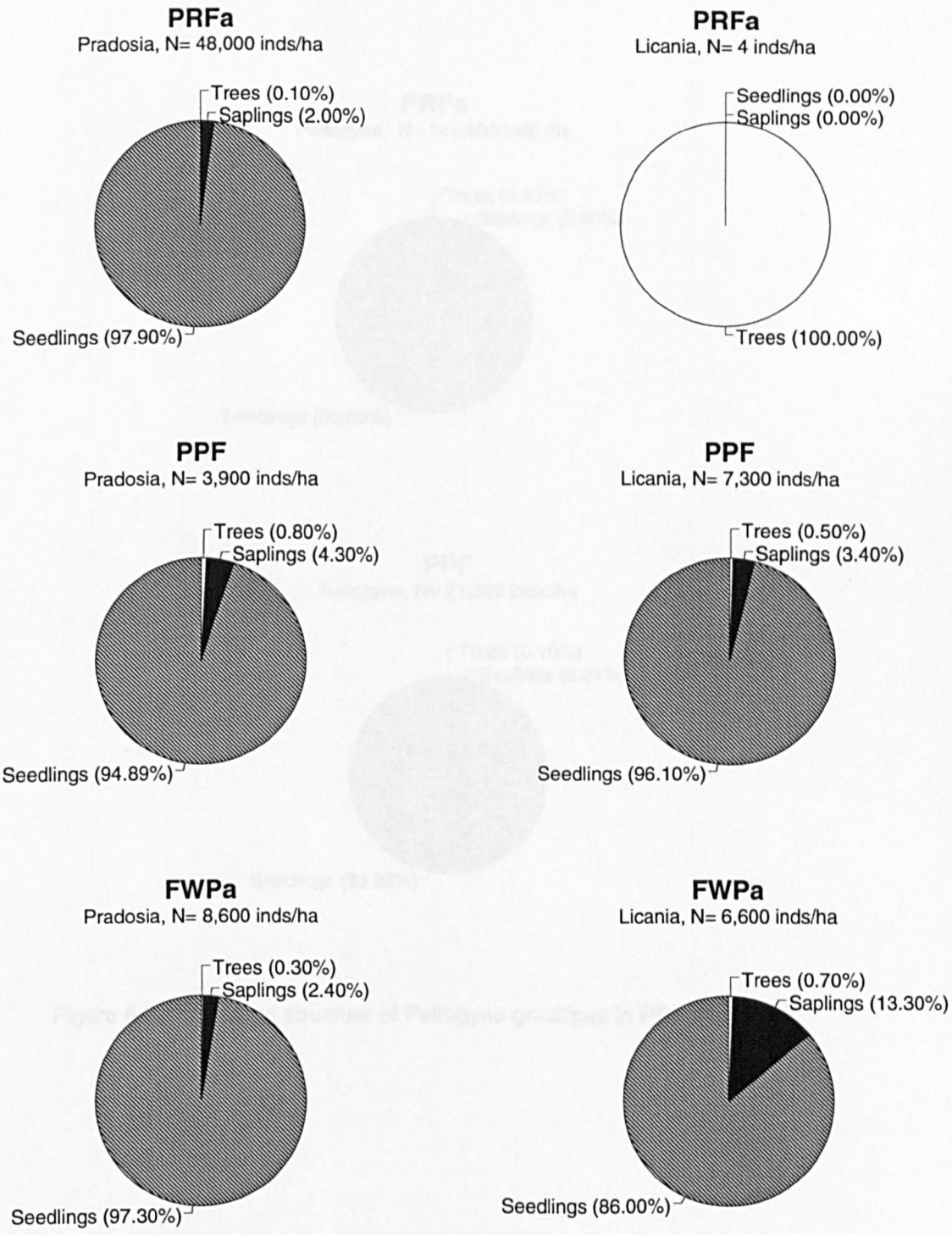


Figure 6.2. Population structure of Pradosia surinamensis and Licania kunthiana in PRF, PPF and FWP.

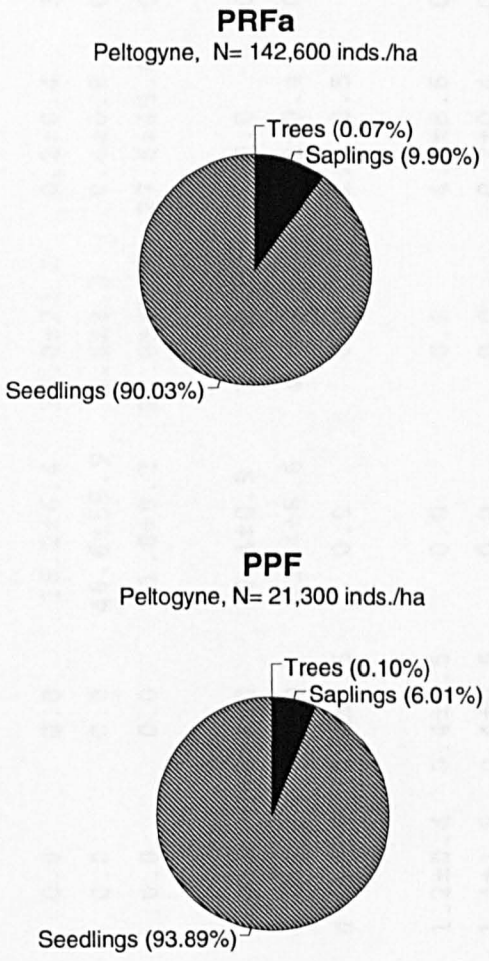


Figure 6.3. Population structure of Peltogyne gracilipes in PRF and PPF.

Table 6.1. Mean number (± SD) of seedlings and saplings per 2 m^2 (seedlings) and 16 m^2 (saplings) sub-plots of the five study species in three forest types on Maracá Island, Brazil. SE= seedlings, SA= saplings.

Plot	*Ecclinusa*		*Lecythis*		*Licania*		*Peltogyne*		*Pradosia*	
	SE	SA	SE	SA	SE	SA	SE	SA	SE	SA
PRFa										
1	0.0	0.0	0.0	0.0	0.0	0.0	16.2±6.4	38.0±22.2	0.2±0.4	3.2±2.6
2	0.6±0.5	0.6±0.5	0.0	0.0	0.0	0.0	46.6±59.9	3.6±3.3	0.4±0.9	0.4±0.5
3	0.2±0.4	0.4±0.8	0.0	0.0	0.0	0.0	11.8±8.2	24.8±15.3	27.6±45.8	0.8±0.8
PPF										
7	0.6±0.8	5.6±5.1	0.2±0.4	0.2±0.4	0.0	0.0	0.4±0.9	1.4±1.7	0.0	0.2±0.4
8	0.6±0.8	2.7±3.4	0.4±0.5	0.2±0.4	0.0	0.0	11.4±8.6	4.6±2.9	0.2±0.4	0.2±0.4
9	1.6±2.2	3.2±2.6	1.0±1.0	1.4±1.7	4.0±4.9	0.4±0.5	0.0	0.0	1.8±2.5	0.0
FWPa										
10	2.6±2.3	0.6±0.8	2.2±2.0	1.4±1.7	1.2±0.4	0.4±0.5	0.0	0.0	4.6±8.6	0.6±0.5
11	3.2±6.6	1.2±2.2	0.0	1.0±1.2	1.4±1.5	0.4±0.5	0.0	0.0	0.2±0.4	0.8±1.3
12	0.0	5.2±4.3	1.0±1.0	0.0	0.8±1.3	3.4±4.6	0.0	0.0	0.0	0.2±0.4

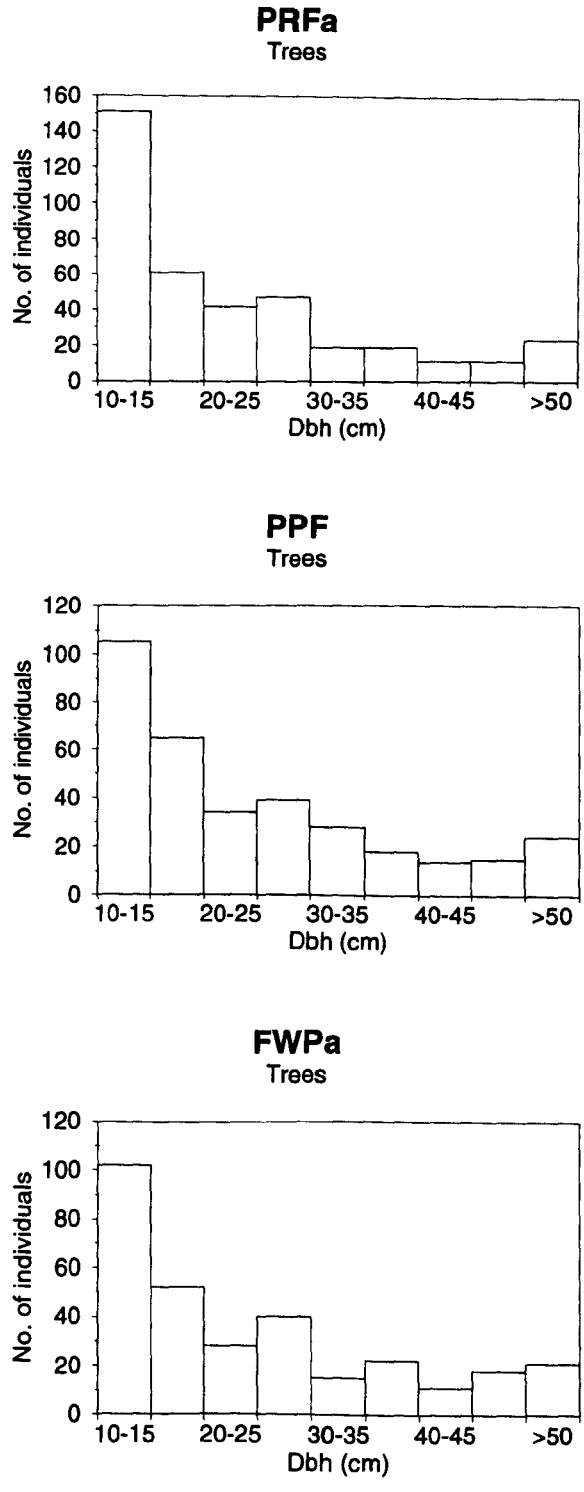


Figure 6.4. Distribution of diameters of trees of all species in PRFa, PPF and FWPa.

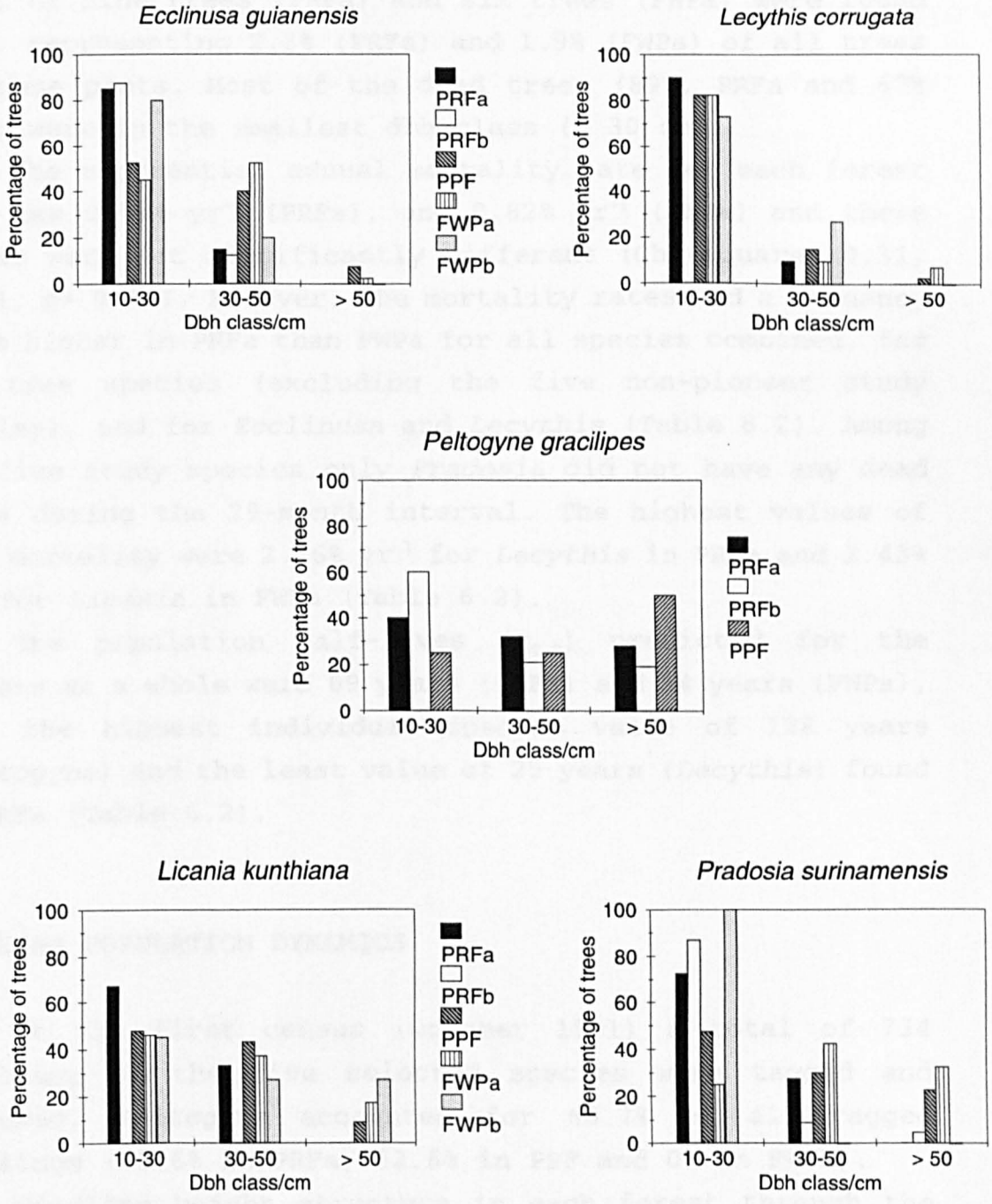


Figure 6.5. Distribution of diameter of trees of five important species in PRF, PPF, and FWP.

TREE MORTALITY

After 29 months (from October 1991 to March 1994), a total of nine trees (PRFa) and six trees (FWPa) were found dead, representing 2.3% (PRFa) and 1.9% (FWPa) of all trees in these plots. Most of the dead trees (89%, PRFa and 67% FWPa) were in the smallest dbh class (< 30 cm).

The exponential annual mortality rate for each forest type was 0.99% yr^{-1} (PRFa), and 0.82% yr^{-1} (FWPa) and these values were not significantly different (Chi-square= 0.31, d.f=1, p> 0.05). However, the mortality rates had a tendency to be higher in PRFa than FWPa for all species combined, for the tree species (excluding the five non-pioneer study species), and for *Ecclinusa* and *Lecythis* (Table 6.2). Among the five study species only *Pradosia* did not have any dead trees during the 29-month interval. The highest values of tree mortality were 2.76% yr^{-1} for *Lecythis* in PRFa and 2.43% yr^{-1} for *Licania* in FWPa (Table 6.2).

The population half-lives ($t_{0.5}$) predicted for the forests as a whole were 69 years (PRFa) and 84 years (FWPa), with the highest individual species value of 128 years (*Peltogyne*) and the least value of 25 years (*Lecythis*) found in PRFa (Table 6.2).

SEEDLING POPULATION DYNAMICS

At the first census (October 1991) a total of 734 seedlings of the five selected species were tagged and measured. *Peltogyne* accounted for 60.7% of all tagged seedlings (72.6% in PRFa, 52.6% in PPF and 0% in FWPa).

Seedling height structure in each forest through the sampling period (Fig. 6.6) showed that most of the seedlings were in the height classes 15-20 cm and 20-25 cm with a strong increase in the number of seedlings in the classes 5-10 cm and 10-15 cm in March 1993 and March 1994. This increase was caused by the high seedling recruitment that

Table 6.2. Number of trees, exponential annual mortality rate (EAMR) for trees (≥ 10 cm dbh) and half-life (year) of the five study species and others over the 29-month period in two forest types on Maracá Island, Roraima, Brazil.

Species	PRFa			FWPa		
	N	EAMR (%yr^{-1})	Half-life*	N	EAMR (%yr^{1})	Half-life
Ecclinusa	45	1.88	37	34	1.23	56
Lecythis	31	2.76	25	21	0	_
Licania	3	0	-	35	2.43	28
Peltogyne	77	0.54	128	0	-	-
Pradosia	36	0	-	25	0	_
Other species	192	0.87	80	194	0.64	108
All species	384	0.99	69	309	0.82	84

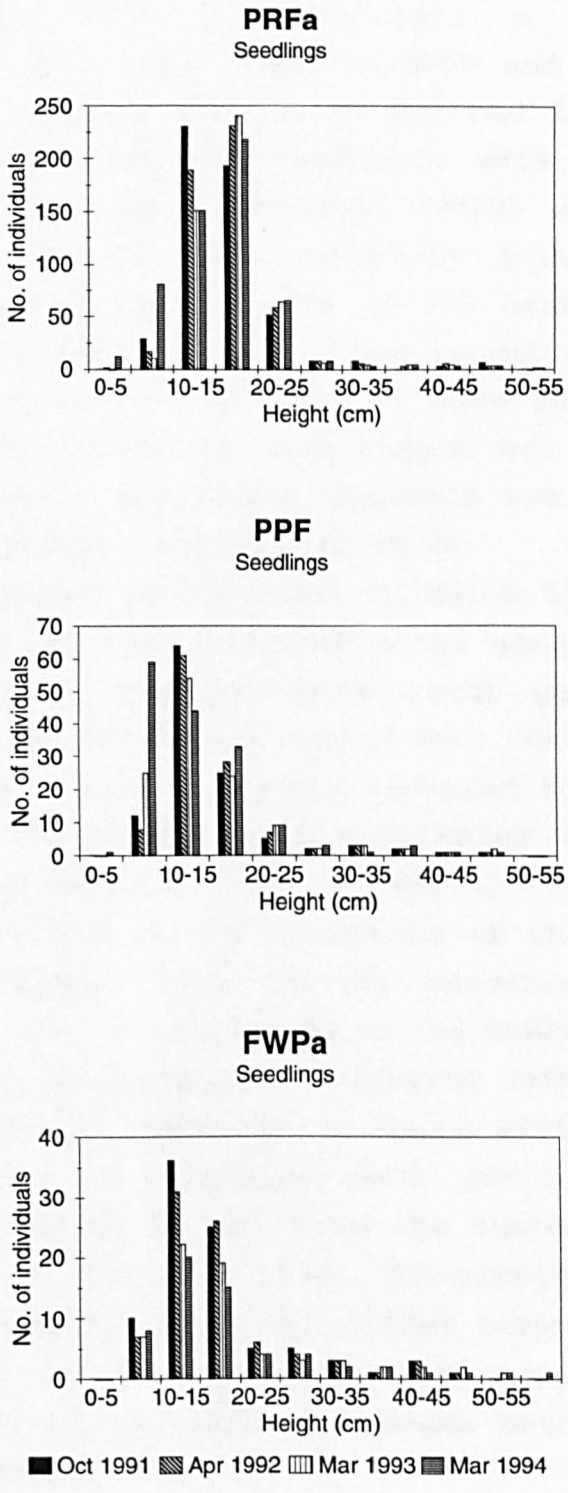


Figure 6.6. Distribution of heights of all seedlings in PRFa, PPF and FWPa

occurred for *Peltogyne* following the mass fruiting of August-December 1992. In March 1993, a total of 81 new *Peltogyne* recruits were found in PRFa and 22 in PPF. Only six recruits in PRFa and two in PPF had leaves damaged by herbivores. The levels of herbivory were in general less than 5%, with only one individual (PRFa) showing 10-25% of leaf damage. In PPF, the herbivory levels for the two damaged seedlings were in the 25-50% herbivory class. In March 1994, the total number of new recruits was higher (413 in PRFa and 63 in PPF) and all of them were *Peltogyne*. In FWPa, only 6 new recruits were tagged and it was, in March 1994, all *Licania*. *Ecclinusa, Lecythis* and *Pradosia* did not produce any recruits during the study.

The *Peltogyne* recruitment in March 1993 reflected an early germination that occurred after some days with rain. However, most of the *Peltogyne* seeds germinated at the beginning of the wet season (April-May 1993). Therefore, it is assumed that the individuals recorded for the first time in 1994 were from seeds which germinated shortly after the last recording date in 1993 (17 March). *Peltogyne* did not flower in 1993 and so the survivors of the 1993 cohort in March 1994 together with the new recruits tagged in 1994 (1994 cohort) can be considered as the number of established seedlings. The percentage of *Peltogyne* undamaged seeds that became established seedlings in March 1994 were calculated from the number of undamaged seeds per m^2 (assessed on 6 March 1993 (Chapter 8) and from the number of established seedlings per m^2 in March 1994. The proportional number of established seedlings did not differ between forests (Chi-square= 1.682, d.f.=1, $p > 0.05$), with a mean of 8.7% (PRFa) and 4.6% (PPF) of the undamaged seeds becoming established seedlings (Table 6.3).

Seedling mortality

In March 1994, after 29 months, 205 seedlings of the

Table 6.3. Mean number of undamaged seeds (m^{-2}) and newly established seedlings (m^{-2}) of *Peltogyne* and the percentage of seeds that became established seedlings in PRFa and PPF on Maracá Island, Roraima, Brazil. For details of the sampling method of undamaged seeds see Chapter 8.

Forest type	Undamaged seeds (a) (m^{-2})	Established seedlings* (b) (m^{-2})	% (100b/a)
PRFa			
1	401	25.7	6.4
2	103	10.3	8.2
3	73	8.4	11.5
Mean			**8.7**
PPF			
7	79	1.6	2.2
8	85	6.0	7.1
9	0**	---	---
Mean			**4.6**

* Established seedlings= number of new seedlings tagged in 1993 that were still alive in 1994 plus new recruits tagged in the 1994 census.

** see Chapter 8.

734 tagged seedlings were dead (27.9%). The seedling mortality over this period in each forest type was 24.5% (PRFa), 32.4% (PPF) and 42.7% (FWPa) with a significant difference in mortality between PRFa and FWPa (Chi-square= 12.80, d.f.= 1, $p \leq 0.001$). EAMR's for all seedlings over 29 months were 11.3 % yr^{-1} (PRFa), 16.4 % yr^{-1} (PPF), and 12.5 % yr^{-1} (FWPa) (Table 6.4). Comparisons among species showed that there is a statistical difference in seedling mortality within PRFa (Chi-square= 10.3, d.f=1, $p \leq 0.005$) and FWPa (Chi-square= 22.1, d.f.= 2, $p \leq 0.001$). These differences were because *Pradosia* had higher mortality than the other species in both PRFa and FWPa (Chi-square= 21.0, d.f.= 1, $p \leq 0.001$, for FWPa). Within species, differences were found for *Peltogyne* (Chi-square= 4.93, d.f= 1, $p \leq 0.05$), as a result of the higher mortality in PPF and for *Pradosia*, as a result of the higher mortality in FWPa (Chi-square= 15.6, d.f.= 2, $p \leq 0.001$). The lowest EAMR's for species were found in censuses that had most of their intervals in the wet season, with the exception of *Pradosia* in FWPa (Table 6.5). Seedling mortality was not height dependent (Fig. 6.7) (Chi-square= 4.84, d.f.= 4, $p > 0.05$) for established seedlings, although smaller seedlings tended to have a higher probability of dying than larger ones. However, most of the *Peltogyne* recruits (62% in PRFa and 54% in PPF) tagged in March 1993 were dead at the 1994 census, with the mortality rates not being different between PRFa and PPF (Chi-square= 1.01, d.f.= 2, $p > 0.05$).

Seedling height growth

The median annual height growths of the species in each forest type over the 29-month measurement period (Table 6.5) were in general similar, with a significant difference only found in the PRFa as a result of a relatively faster growth of *Peltogyne* (Mann-Whitney U test= 65237.0, d.f.= 1, p= 0.000). Within species, the analyses did not show any

Table 6.4. Exponential annual mortality rate (EAMR) over a 29-month period for seedlings of the five study species in three forest types on Maracá Island, Roraima, Brazil. Only seedlings tagged at the first census (October 1991) were included.

Species	PRFa		PPF		FWPa	
	EAMR % yr^{-1}	N	EAMR % yr^{-1}	N	EAMR % yr^{-1}	N
Ecclinusa	38.3	5	17.0	15	14.9	30
Lecythis	-	0	23.4	7	8.1	17
Licania	-	0	8.8	21	8.1	17
Peltogyne	9.6	385	17.0	60	-	0
Pradosia	17.3	141	25.3	11	59.7	25
All species	11.3	531	16.4	114	12.5	89

Table 6.5. Exponential monthly mortality rate (% $month^{-1}$) calculated for four censuses for seedlings of the five study species, tagged in October 1991 in three forest types on Maracá Island, Roraima, Brazil.

Species	April 1992	July 1992	March 1993	March 1994
PRF				
Ecclinusa	4.31	0	4.40	0
Peltogyne	0.89	0.54	1.02	0.64
Pradosia	2.46	0	1.31	1.18
PPF				
Ecclinusa	0	0	0.88	2.43
Lecythis	0	0	0	3.65
Licania	0	0	1.26	0.90
Peltogyne	0.86	0.57	1.88	1.42
Pradosia	1.56	0	1.31	2.83
FWP				
Ecclinusa	1.72	0	0.49	1.64
Lecythis	1.01	0	1.65	0
Licania	1.01	0	1.65	2.43
Pradosia	4.82	9.16	3.04	3.41

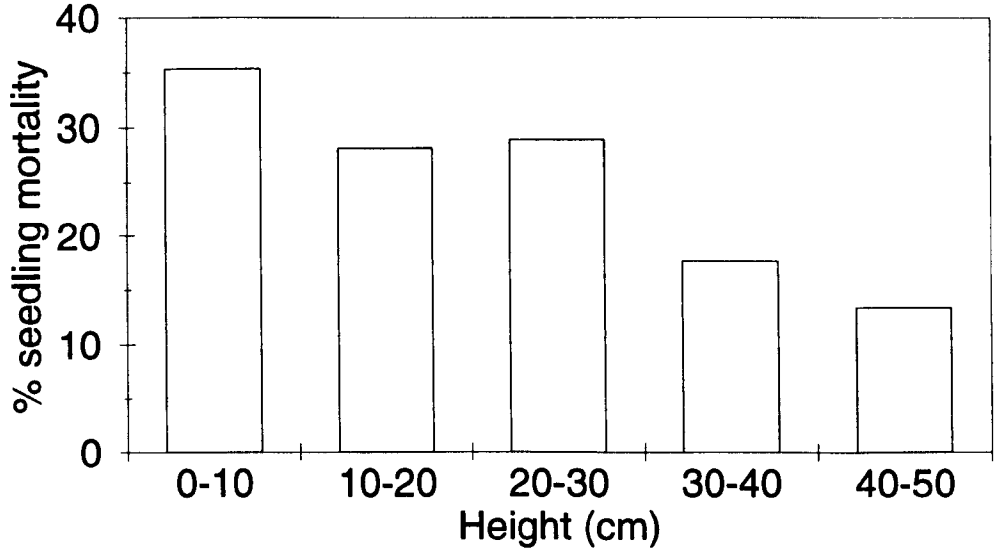


Figure 6.7. Histogram of the percentage mortality for different height classes of all seedlings for all studied forest types over 29 months on Maracá Island, Brazil.

statistically significant differences of seedling height growth rates among forests.

The percentages of suppressed individuals which showed zero or negative net height growth over 29 months in each forest were 22% (PRFa), 14% (PPF) and 24% (FWPa). The differences were not significant (Chi-square= 1.814, d.f.=2, $p > 0.05$). The number of suppressed individuals varied from 7.1% (*Lecythis* in FWPa) to 33.3% (*Pradosia* in FWPa) (Table 6.6). Only for PRFa (for inter-specific comparisons) and for *Peltogyne* (for intra-specific comparisons) there were sufficient numbers of suppressed individuals to permit statistical analysis. For PRFa, there was no difference in the proportion of suppressed individuals between *Pradosia* and *Peltogyne* (Chi-square= 3.666, d.f.= 1, $p > 0.05$). The proportion of suppressed individuals of *Peltogyne* in PRFa was also not different from the proportion in PPF (Chi-square= 2.008, d.f.= 1, $p > 0.05$).

Seedlings of all species had significant year-to-year variation in height growth, but there was no clear pattern among species (Table 6.7). However, the highest growth rate tended to be during the March 1993-March 1994 interval.

Comparisons between the gap and PRFa

Both *Peltogyne* and *Pradosia* showed higher median annual growth rates in the gap (4.52 cm/yr, *Peltogyne* and 1.58 cm/yr, *Pradosia*) than in PRFa (0.63 cm/yr, *Peltogyne* and 0.32 cm/yr, *Pradosia*) (Mann-Whitney test, $p< 0.001$ for both species). *Peltogyne* had faster growth than *Pradosia* in the gap (Mann-Whitney test, $p< 0.01$).

From August 1991 to March 1994 five individuals (*Peltogyne*) and nine (*Pradosia*) died in the gap. The percentage mortality for both species did not differ between gap and under closed canopy (Chi-square= 0.002 (*Peltogyne*) and 0.58 (*Pradosia*), d.f.= 1, $p>0.05$). The inter-specific analysis for mortality showed that species also had similar

Table 6.6. Median annual height growth, maximum height growth, median difference in leaf number, and the percentage of suppressed individuals in the 29-month period (October 1991-March 1994) of seedlings of five tree species in three forest types on Maracá Island, Roraima, Brazil.

Species	Med. (cm/yr)	Max. (cm)	Med. leaf no.	% supp.	N
PRFa					
Peltogyne	0.84	11.5	-1.00	16.0	306
Pradosia	0.42	6.5	-1.00	24.7	93
PPF					
Ecclinusa	0.46	7.6	0.00	18.2	10
Lecythis	0.21	7.0	-0.50	25.0	4
Licania	0.84	3.5	1.00	12.5	16
Peltogyne	1.00	6.9	-1.00	7.5	40
Pradosia	1.15	8.3	-1.00	16.7	6
FWPa					
Ecclinusa	0.63	14.7	-2.00	23.8	21
Lecythis	0.63	3.6	1.00	7.1	14
Licania	1.25	8.0	3.50	20.0	10
Pradosia	0.19	1.7	-2.00	33.3	6

Table 6.7. Among-year variation in height growth rates of seedlings surviving from October 1991 to March 1994 in three forest types on Maracá Island, Roraima, Brazil.

Species	Median annual height growth (cm)			N	p[ε]
	October-April 1992	April-March 1993	March-March 1994		
PRFa					
Peltogyne	2.03	0.00	2.13	306	***
Pradosia	0.00	0.61	1.01	93	n.s
PPF					
Ecclinusa	0.00	0.55	0.55	10	n.s
Lecythis	0.00	0.00	0.50	4	n.t
Licania	0.00	1.01	1.66	16	**
Peltogyne	1.01	0.00	1.50	40	***
Pradosia	0.00	0.00	2.12	6	n.s
FWPa					
Ecclinusa	0.00	1.11	0.44	21	*
Lecythis	0.00	0.72	0.90	14	n.s
Licania	0.00	1.05	0.40	10	n.s
Pradosia	0.00	1.00	-0.30	6	*

n.t= not tested, n.s= not significant ($p > 0.05$).
[ε] Probabilities are for Friedman non-parametric two-way anova.
* ≤ 0.05, ** ≤ 0.01, *** ≤ 0.001.

mortality in the gap (Chi-square= 1.49 , d.f.= 1, p> 0.05). From August 1991 to August 1992 most of the deaths in the gap were during the dry season, when one seedling of *Peltogyne* and three individuals of *Pradosia* died.

The proportional number of suppressed individuals for *Peltogyne* did not differ between the gap and under closed canopy (Chi-square= 3.58, d.f.= 1, p> 0.05). However for *Pradosia*, individuals growing under closed canopy suffered more suppression than those growing in the gap (Chi-square= 5.43, d.f.= 1, p≤ 0.025).

SAPLING POPULATION DYNAMICS

A total of 548 individuals greater than 0.5 m tall and smaller than 31.4 cm gbh were tagged and measured in October 1991, from this total, 67.7% were *Peltogyne*. This species accounted for 91.6% (PRFa) and 29.2% (PPF) of all tagged individuals. Three hundred and twenty-two individuals (58.7%) were sampled in size class 1 (individuals > 0.5 cm tall and ≤ 2.0 cm gbh) and 226 (41.3%) in size class 2 (individuals > 2.0 cm gbh and < 10.0 gbh). The proportion of the number of individuals in these two size classes (Table 6.7) differed among forests (Chi-square= 18.603, d.f.= 2, p≤ 0.001). This difference was due to the highest number of individuals in the smallest class in PPF (Chi-square= 17.23, d.f.=1, p≤ 0.001).

Measurements of all tagged saplings in the three forest types (Fig. 6.8) showed that most of saplings were in the smallest class for both gbh and height categories. However, FWPa had a high number of individuals in the 150-175 cm height class, showing a different pattern when compared with the other forests. All forest types showed a similar sapling distribution in the gbh classes. These figures suggest that over the 17 months there was no recruitment of saplings in any forest type and although PRFa and FWPa had some individuals appearing in the smallest size class (40-50 cm

Table 6.8. Total number of saplings of five study species tagged in October 1991 and the percentage of individuals in size class 1 (> 0.5 m tall and ≤ 2 cm gbh) and size class 2 (> 2 cm gbh and < 31.4 cm gbh) in three forest types on Maracá Island, Roraima, Brazil.

Species	PRFa			PPF			FWPa		
	N	1	2	N	1	2	N	1	2
		%			%			%	
Ecclinusa	5	60	40	56	73	27	37	62	38
Lecythis	3	0	100	9	78	22	8	37	62
Licania	---	---	---	6	83	17	21	67	33
Peltogyne	340	53	47	31	77	23	---	---	---
Pradosia	23	39	61	4	100	0	5	60	40
Total	371	53	47	106	76	24	71	60	40

Table 6.9. Exponential annual mortality rate (EAMR) for saplings over a 17-month period for the five study species in three forest types on Maracá Island, Roraima, Brazil.

Species	PRFa % yr^{-1}	PPF % yr^{-1}	FWPa % yr^{-1}
Ecclinusa	0	0	0
Lecythis	0	18.02	9.58
Licania	-	0	3.50
Peltogyne	6.62	0	-
Pradosia	3.19	0	0
All species	6.46	1.36	2.05

tall) it was not a result of recruitment but a result of a breakage of the main stems from individuals that resprouted later.

Sapling mortality

A total of 36 individuals died between October 1991 and March 1993, corresponding to a 6.4% mortality. The percentage mortality over the 17-month interval among forests varied from 0.9% (PPF) to 8.6% (PRFa) (Table 6.9). These differences were statistically significant (Chi-square=7.97, d.f.=2, $p \leq 0.005$), with PRFa having more deaths than PPF (Chi-square= 5.65, d.f.= 1, $p \leq 0.025$), but not significantly more than FWPa (Chi-square= 2.83, d.f.= 1, $p > 0.05$).

The percentage mortality of all species and forests was higher for individuals in size class 1 than in size class 2 (Chi-square= 4.73, d.f.=1, $p \leq 0.05$), with 28 individuals from the total of 36 dead individuals (77.8%) in the size class 1. Most of deaths (86.1%) were *Peltogyne*. In contrast, *Ecclinusa* did not have any dead individuals between October 1991 and March 1993.

Sapling growth

Important changes in growth occurred only in height classes, with no change observed for gbh classes (Fig. 6.8). Therefore, the growth rate of each species was calculated only from individuals greater than 0.5 m tall and smaller than 2.0 cm gbh. The values are shown in Table 6.10. The interspecific analysis in each forest type showed that in PRFa *Pradosia* grew faster than *Peltogyne* (Mann-Whitney test, p= 0.02). These species did not differ in PPF, although the Kruskal-Wallis Anova showed a significant difference among species (H= 9.95, d.f.= 4, p= 0.04). This difference was

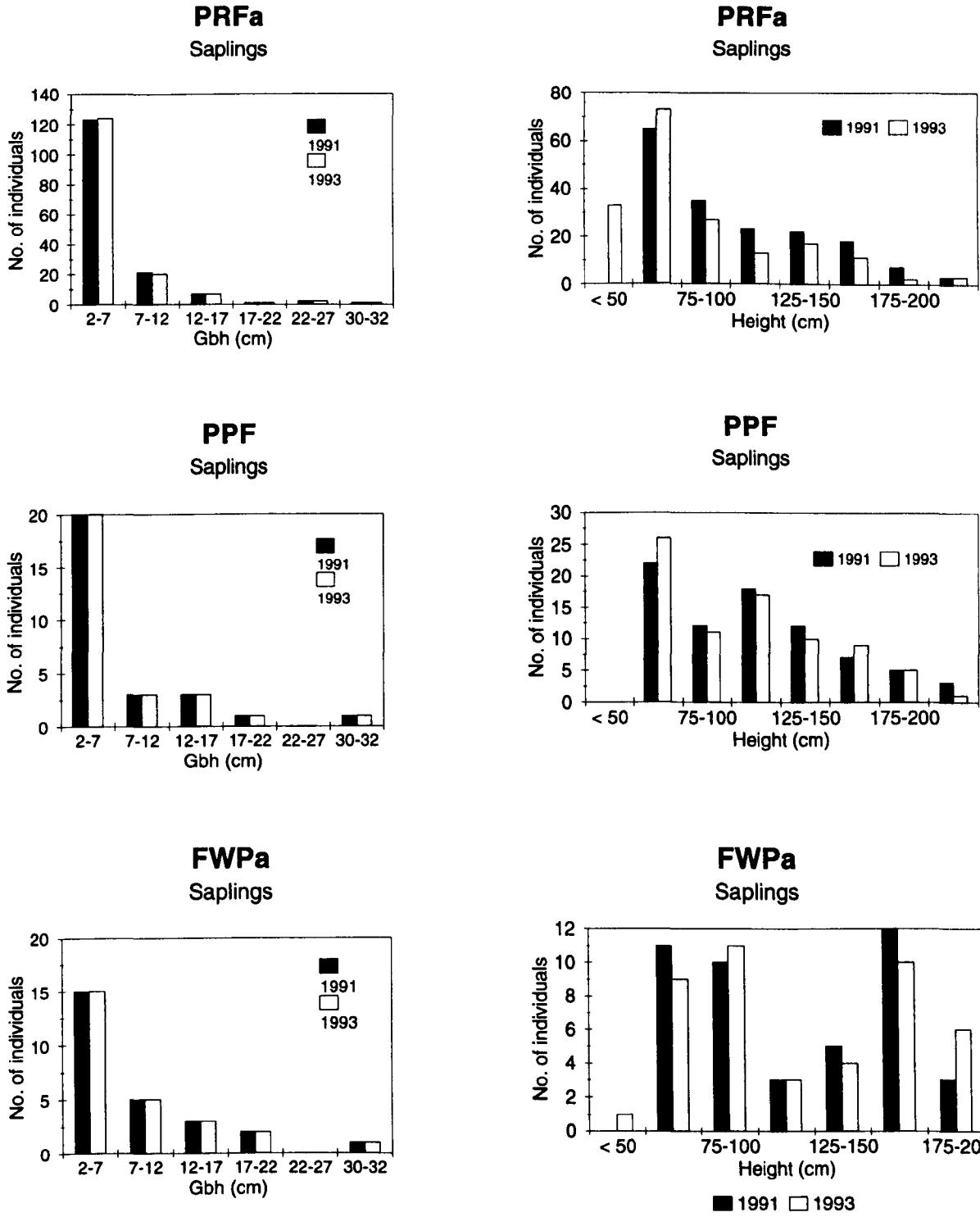


Figure 6.8. Distribution of girths and heights of saplings (survivors of the entire period, 1991-93) in PRFa, PPF, and FWPa, at first and last censuses.

Table 6.10. Median annual height growth of saplings (< 2.0 cm gbh), maximum height growth, and the percentage of suppressed individuals in 17 months from October 1991 to March 1993 in five tree species in three forest types on Maracá Island, Roraima, Brazil.

Species	Med. (cm/yr)	Max. (cm)	Supp. (%)	N
PRFa				
Peltogyne	-2.15	14.0	74.7	166
Pradosia	1.08	10.0	25.0	8
PPF				
Ecclinusa	1.08	13.0	39.0	41
Lecythis	1.43	9.0	20.0	5
Licania	3.58	6.0	40.0	5
Peltogyne	-2.51	7.0	66.7	24
Pradosia	0.00	16.0	80.0	5
FWPa				
Ecclinusa	1.43	12.0	34.8	23
Lecythis	3.23	6.0	0	2
Licania	3.58	11.0	7.7	13
Pradosia	1.43	3.0	33.3	3

mainly related to *Ecclinusa* which grew faster than *Peltogyne* (Mann-Whitney test, p= 0.006). In FWPa, owing to small samples, comparisons were carried out only between *Ecclinusa* and *Licania*, with *Licania* showing a higher growth rate than *Ecclinusa* (Mann-Whitney test, p= 0.04). Among-forest-type analyses showed that none of the five species had different growth rates.

The percentages of suppressed individuals over a 17-month period were 72.8% (PRFa), 48.7% (PPF) and 12.2% (FWPa) (Table 6.10). They differed statistically (Chi-square= 53.68, d.f= 2, $p \leq 0.001$), with this difference mainly due to the lower growth suppression in FWPa than in PRFa (Chi-square= 51.33, d.f.= 1, $p \leq 0.001$) and in PPF (Chi-square= 13.99, d.f.= 1, $p \leq 0.001$). Those differences are mainly due to the high proportion of suppressed *Peltogyne* individuals found in both PRFa and PPF.

Intraspecific analyses for growth suppression were carried out only for *Ecclinusa* and *Peltogyne* which did not show any difference between forest types. There were too few individuals of *Lecythis*, *Licania* and *Pradosia*, to make a statistical test but it is noteworthy that *Licania* and *Pradosia* had the highest percentage of suppressed individuals in PPF, with *Lecythis* showing similar percentages between forests (Table 6.10).

CAUSES OF MORTALITY AND SUPPRESSION

The tree mortality ($\geq$ 10 cm dbh) caused by fallen trees or branches was 33% in both forest types (PRFa and FWPa). The causes of the other deaths is unknown. Most of the dead trees (78%, PRFa and 67% FWPa) were in the smallest dbh class ($\leq$ 30 cm) and 89% (PRFa) and 67% (FWPa) of the tree mortality occurred in understorey species.

For all seedlings and saplings of the five study species, 3% (seedlings) and 19.4% (saplings) of the deaths were clearly caused by litterfall (including large wood).

Many of the stems found dead (76%, seedlings and 75% saplings) were still standing, with most deaths occurring in the dry season. The cause of these deaths is tentatively attributed to drought. For the other deaths the cause of the mortality was unknown. During the 29-month study no evidence of seedlings dying as a result of mammalian predation was found. The relationship between the seedling mortality of *Peltogyne* and *Pradosia* and herbivory will be discussed in Chapter 9.

The stems of *Peltogyne* saplings suffered much termite attack over the 17-month period, with 19% of stems recorded as being attacked by termites. Some of the attacked stems (37%) were still alive, but had part of the stem dried and damaged. Most of the dead *Peltogyne* saplings (61%) were also found attacked by termites. Only 1.7% of the saplings of the other four species were attacked by termites. The number of termite nests on trees per hectare in each forest type were higher in PRFa (120) and in PPF (105) than in FWPa (83), with 30% (PRFa) and 44% (PPF) of the *Peltogyne* trees having a termite nest. Most of the nests were of *Microcerotermes arboreus* or a species of *Nasutitermes* (A. Bandeira, personal communication). Most of the suppressed saplings, especially for *Peltogyne*, had a negative growth rate (80.8% in PRFa, 69,2% in PPF, and 60.0% in FWPa). This resulted from stem breakage caused by termite attack in the part of the stem that was dead or damaged (15%); from litterfall (9%); by the combination of these two factors (16%); or from an unknown factor (60%).

DISCUSSION

POPULATION STRUCTURE OF THE SPECIES

As already described in Chapter 4, the forest community as a whole showed the typical structure of undisturbed

forests, with the majority of trees in the smallest classes (Whitmore 1984). Most of the study species had a large number of seedlings, saplings and trees, indicating good regeneration. However, *Lecythis* and *Licania* did not show this pattern in PRFa, occurring only as trees and saplings (*Lecythis*) and as trees (*Licania*). Those figures suggest that these species are declining in PRFa, possibly owing to interspecific competition with expanding *Peltogyne*.

Peltogyne was by far the most abundant species in PRFa in all size classes, and also had a large number of individuals as seedlings and saplings in PPF (although there was much variation in numbers among the three replicate PPF plots). Therefore, *Peltogyne* seems to have a stable, actively regenerating population.

Tree mortality

Tree mortality rates calculated arithmetically and by the log model (Swaine & Lieberman 1987) for Maracá forests (0.98%/yr and 0.99%/yr in PRFa and 0.81%/yr and 0.82%/yr in FWPa) were very similar. They were similar to the rates (log model) found for the FWPab plots (mean= 0.77%/yr, ranging from 0.19%/yr to 1.25%/yr , calculated over four years (1987-1991) J. Thompson personal communication). They were also close to the rates (arithmetic calculation) found in other studies for undisturbed sites in Amazonia (0.96-1.22%/yr, Rankin-Merona *et al.* 1990 and 1.3%/yr, Carvalho 1992) than for logged-over Amazonian forest (2.8%/yr, Silva 1989 and 3.1%/yr and 4.3%/yr, Carvalho 1992). The mortality rates found for Maracá forests were also more similar to the rates found by Lang & Knight (1983) (1.04%/yr) for a lowland forest in Barro Colorado, Panama and by Nicholson (1965) (1.0%/yr) for a mature forest in Sepilok, Malaysia than for a lowland forest at La Selva (2.03-2.34%/yr, Lieberman *et al.* 1990); for a gallery forest in central Brazil (3.5%/yr, Felfili 1993); and for a dipterocarp forest in Malaysia

(2.02%/yr, Manokaran & Kochummen 1987). The stand half-life of 69 years (PRFa) and 84 years (FWPa) based on 1991-94 mortality data were similar to the values found for a *terra firme* forest in central Amazonia (82-104 years, Rankin-Merona *et al.* 1990) and were much higher than the values found for a primary forest at La Selva (34 years, based on 1969-82 mortality data or 30 years, based on 1982-85 data (Lieberman *et al.* 1990); for a gallery forest in central Brazil (20 years, Felfili 1993); and for a dipterocarp forest in Malaysia (35 years, Manokaran & Kochummen 1987). The tree mortality data for PRFa and FWPa are based on a short period (29 months) and a small sample size (0.75 ha/forest type) and so the comparisons above should be treated with caution. However, they suggest that Maracá forests have comparatively stable stands with a low annual mortality rate.

Clark & Clark (1992) studying six non-pioneer tree species in primary tropical forest at La Selva, Costa Rica suggested that emergents and canopy species have substantially lower rates of mortality than do understorey trees that reach 10 cm dbh. They concluded that community-wide values may mask a diversity of mortality patterns for different types of trees. Manokaran & Kochummen (1987) found similar results for a primary forest in Malaysia. Recently, Korning & Balslev (1994) also found a similar trend for a lowland forest in Amazonian Ecuador. The results for the Maracá forests (table 6.1) also support this hypothesis, with canopy tree species having a lower mortality rate than understorey tree species.

Seedling mortality

Some authors (e.g. Sarukhán 1978, Clark & Clark 1987, Turner 1990) have found that seedling mortality is size dependent. However, the percentage mortality of established seedlings for all five study species in Maracá forests was

not size dependent, although there was a tendency for the smallest individuals to have a high mortality. The *Peltogyne* data for establishing seedlings from the early recruitment in March 1993 showed a high mortality (62%, PRFa and 54%, PPF) in the first year, indicating that most of the seedling mortality occurs in the first year.

Early seedling survival varies widely and it depends on species, habitat, and cohort (Schupp 1990). The annual mortality of early recruits of *Peltogyne* was lower than those found by Lieberman & Lieberman (1987) for a community-wide seedling cohort at La Selva, Costa Rica (80% or more). However, it is within the range reported by Sarukhán (1980) for eight species (13.9 to 78.6%), although these values are for 6-month mortality.

Seedling mortality seems to be highest during the dry season (October to March) (Table 6.4) and may be related to a water shortage. Lieberman & Lieberman (1987) for a community-wide census at La Selva, Miller (1991) for the tree species *Hymenea parvifolia* in a FWPa on Maracá Island and Nascimento & Hay (1994) for the tree species *Metrodorea pubescens* in a gallery forest in central Brazil also related seedling mortality to drought. Plants exposed to water stress are considered more vulnerable to herbivory and pathogens (Grime 1979, Louda *et al.* 1987) as well as the physiological effects of a water shortage.

Sapling mortality

A clear decline in mortality rates through sapling size classes was observed in PRFa, PPF and FWPa for all five study species combined. Other studies of canopy species in tropical rain forest have found similar results (Uhl 1982, Lieberman *et al.* 1985, Clark & Clark 1992).

Causes of mortality

Several studies have demonstrated that physical damage due to tree, branch and litter fall is an important cause of plant mortality in the tropical forests (Uhl 1982, Aide 1987, Clark & Clark 1987, Clark & Clark 1991). The results of this study confirm that fact, with the mortality levels caused by a tree or branch fall increasing from 3% for seedlings, through 19.4% for saplings to 33% for trees.

Seedling and sapling growth

Several studies have found that higher light availability (e.g. Augspurger 1984, Popma & Bongers 1988, Molofsky & Fisher 1993) results in larger plants. This environmental variable is in general related to gap size or canopy structure (Whitmore 1984). Although no measurements have been made on Maracá, PRFa as a deciduous forest could be considered to have more light than FWPa, especially during the dry season. However, as shown in the vegetation profile diagrams (Chapter 4), PRFa has a better developed understorey and so the ground seems to be just as shaded under it as in the FWPa. The intra-specific analyses of the median annual height growth for seedlings and saplings showed that all the five study species grew at similar rates among forests, a surprising result in view of the complex interaction of environment and biotic factors. The seedlings and saplings of the five study species had low growth rates and showed a high intra-specific variation, as found in other studies for tropical species (e.g. Clark & Clark 1987 and 1992, Turner 1990), with some individuals showing zero or negative growth and others growing well.

Several studies (Hartshorn 1980, Connell 1978, Whitmore 1984, Brokaw 1985, Denslow 1987,) have shown that gap formation plays an important role in the species composition and structure of tropical rain forests, with species in

general growing faster in gaps (Augspurger 1984, Popma & Bongers 1988, Turner 1990, Molofsky & Fisher 1993). The results from the gap analyses showed that *Peltogyne* and *Pradosia* grow better in the gap than under the canopy, with similar mortality rates between sites, indicating that gap formation could be an important factor in the dynamics of these species. Although, there are no data available on the number of gaps produced annually on Maracá Island, they could be considered similar among forest types, since tree mortality did not differ between forests.

CONCLUSION

The PRFa, PPF and FWPa have stable stands with a low annual tree mortality rate. In FWPa and PPF, the five most abundant tree species in those forests occurred with the large number of individuals in the smallest size classes, indicating good regeneration. However, in PRFa *Licania* and *Lecythis* are apparently declining and are relicts in an expanding *Peltogyne* forest.

Peltogyne has a stable, regenerating population in PRFa and is clearly a monodominant forest with a persistent dominant (*sensu* Connell & Lowman 1989).

Chapter 7. Soil and plant changes at the *Peltogyne*-rich forest boundary.

INTRODUCTION

Several factors such as climate, soils, topography, hydrology and man influence the structure and floristics of tropical vegetation (e.g. Crow & Gribal 1979, Gartlan *et al.* 1986, Newbery *et al.* 1986, Furley & Ratter 1990, Liberman *et al.* 1985, Oliveira-Filho *et al.* 1994a and 1994b) and so the form and location of boundaries between different vegetation types. The boundaries, with their complex environment, are of particular interest because they provide evidence for shifting vegetation patterns, indicating forest advance, retreat or a potential for regeneration (Furley & Ratter 1990).

Ninety-five percent of Maracá Island is covered by forest and the remaining 5% by savanna (Milliken & Ratter 1989). Some ecological studies have been carried out on forest-savanna boundaries on Maracá (Furley & Ratter 1990, Thompson *et al.* 1992b). However, no study had been done on the boundaries between PRF and FWP. Although PRF is recognised as one of the most common forest types on Maracá (Milliken & Ratter 1989), there are just brief comments on the PRF-FWP boundaries (Furley & Ratter 1990). PRF forms a clear boundary with FWP, easily distinguished during the dry season because of the deciduous crowns of *Peltogyne* (Fig. 3.2).

The work in this chapter aimed to assess the changes in the soil and floristic composition in a transition between PRF and FWP, to explain the dynamic processes which are currently shaping the PRF, and to test the hypothesis that the *Peltogyne* boundary is advancing or contracting rather than being static.

MATERIALS AND METHODS

STUDY SITE AND TRANSECT LOCATION

This study was carried out on the PRFa. Three parallel transects (180 m x 20 m) were randomly located across the *Peltogyne* stand (Fig. 3.4). The transects were sub-divided into 18 20 m x 10 m quadrats. In all the transects, the first quadrat was positioned near a seasonal stream at the base (c. 1.3 m a.s.l) of a gentle (c. 7°) slope and the last one at the top on a plateau about 25 m higher than the base. The transects crossed the centre of the *Peltogyne* stand about 50 m from the first quadrat. *Peltogyne* occurred in some quadrats on the plateau indicating that the transects did not reach the FWP and so the boundary is in fact between PRF and PPF.

SOIL SAMPLING AND ANALYSIS

A soil pit was dug in the first and last quadrat of transect 1. The pit from PRF2 was used to characterise the soil of the middle point of the transect, since this plot was located parallel to transect 1 and its pit was about 45 m perpendicular from the central point of the transect. The soil profile descriptions are given in Table 7.1.

Three soil surface (0-10 cm) samples were collected in each quadrat of each transect in March 1992, one from the middle point of each side and the other in the mid-point of the quadrat. The samples from the same quadrat were pooled, air-dried and sieved through a 2-mm mesh and 150-g subsamples were stored for up 6 months in air-tight polythene bags until shipment to Stirling. Soil analyses for pH, loss on ignition, total acidity, exchangeable cations, and total and extractable phosphorus were as described in Chapter 4. Total nitrogen was analysed only for the soil pit samples. Particle size was determined for samples from the

soil pit and for three soil surface samples in each transect (quadrats 1, 9, 18, 19, 28, 36, 37, 46 and 54).

FLORISTIC INVENTORY

All trees and lianas (≥ 10 cm dbh) were marked with a permanent aluminium tag in September 1991 and measured for gbh. For trees with large buttresses or prop roots reaching more than 1.3 m high the diameter were measured 20 cm above these protrusions. For the few cases of trees with multiple stems, each stem was measured separately and the sum of the basal areas was considered the tree basal area. During the enumeration, each tree was identified as far as possible and confirmed from collected specimens. Voucher specimens are lodged in the Herbarium of Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil and the Herbarium of the Royal Botanic Gardens (E), Edinburgh, Scotland. Seedlings (≤ 0.5 m tall) and saplings (> 0.5 m tall, < 10 cm dbh) were sampled in 18 subquadrats of 2 m x 0.5 m (seedlings) and nine subquadrats of 4 m x 4 m (saplings).

The floristic data were analysed using the FITOPAC package in the same way as described in Chapter 4.

FLORISTIC ORDINATION AND CLASSIFICATION

Detrended Correspondence Analyses (DCA) (Hill & Gauch 1980) (see Chapter 5 for details) based on the density and basal area data of all quadrats from each transect including all species were made for trees ≥ 10 cm dbh. The CANOCO program version 3.10 (ter Braak 1988) was used for the analyses. The data were log transformed prior to the analysis to reduce the variance. The relationship between species abundances and soil variables was analysed by a DCCA. The matrix of the environmental variables consisted of the values for nine soil variables (loss-on-ignition, pH, P extractable, K, Ca, Mg, Mg/Ca, Al, H). For the species

matrix all species were included. The significance of the relationship between species and the environmental variables was tested by the Monte Carlo permutation test (ter Braak 1988, 1990).

A TWINSPAN classification of all quadrats of the transects based on all species was made for trees ≥ 10 cm dbh. The analyses were made for basal area and density data. Pseudospecies cut-levels were 0, 2, 3, 4 and 6 for density and 0, 0.04, 0.08, 0.2 and 0.6 m^2 per quadrat for basal area.

RESULTS

SOILS

A description of the soil transect is given in Table 7.1. Chemical and textural data for each pit (Table 7.2) and for surface soils (Table 7.3-7.5) showed that the soils are poor in nutrients, sandy and acid and very similar among and within transects.

STRUCTURAL AND FLORISTIC DATA

The structure of the PRF forest on the transects (Table 7.6) was similar to the PRF plots (see Chapter 4 for details), with within-transect values for basal area varying from 25.1 to 35.7 m^2/ha and for density from 431 to 511 trees/ha. The transects had similar family diversity values, with the coefficients of family similarity between transects always higher than 70% (Table 7.7). Caesalpiniaceae and Sapotaceae were the most important families in all transects. A list with the species names and authorities is given in Appendix 2. The number of species in the transects varied from 35 to 38, with about 35% of species similarity

Table 7.1. Description of each soil pit made in the study transect 1. Colour determination made on wet samples.

Pit 1- transect 1 qradrat 1 (19 March 1993)- Base of hill, gently sloping, occasionally flooded, very near to "Buritizal" (*Mauritia flexuosa*, Palmae) edge (2 m).

0-22 cm - Loamy sand 10 YR 3/2 (very greyish brown), weak fine sub-angular blocky structure, soft, very frequent fine and medium roots. Many pores, very good porosity, with a clear boundary.

22-37 cm - Loamy sand 10YR 5/2 (greyish brown), weak fine sub-angular blocky structure, soft. Frequent fine roots and medium roots. Many pores, good porosity, clear boundary.

37-66 cm - Loamy sand 10 YR 6/2 (light brownish grey),weak fine sub-angular blocky structure, soft. Few fine and medium roots. Common pores, good porosity, clear boundary.

66-77 cm - Loamy sand 10 YR 7/1 (light grey), common mottles 5 Y 6/3 (pale olive), weak fine sub-angular blocky structure, soft. Very few fine roots. Common pores, good porosity, abrut boundary.

77-89+ cm- Loamy sand 2.5 Y 5/4 (light olive brown), very strong large angular blocky structure, very hard. No roots. Very few pores, poor porosity. Common small and large stones with few large ones to.

Pit 2- plot PRF2 (18 March 1993)- Gently sloping

0-10 cm - Loamy sand 10 YR 4/2 (dark greyish brown), weak fine sub-angular blocky structure, very soft. Very frequent fine and medium roots. Very good porosity, with a clear boundary.

10-35 cm - Loamy sand 10YR 5/3 (brown), moderate medium sub-angular blocky structure, soft. Common fine and medium roots. Little charcoal at 30 cm depth. Good porosity, gradual boundary.

35-62 cm - Loamy sand 10 YR 6/3 (pale brown), few mottles 7.5 YR 6/6 (light red),moderate medium sub-angular blocky structure, slightly hard. Common fine roots. Good porosity, clear boundary.

62-120+ cm - Loamy sand 10 YR 7/1 (light grey), common mottles 7.5 YR 6/6 (light red), strong moderate large angular blocky structure, slightly hard. Common fine roots. Good porosity.

Pit 3- transect 1 quadrat 18 (18 March 1993)- Plateau, gently sloping, near (20 m) a small patch of "Buritizal" (*Mauritia flexuosa*, Palmae). Termite channels in all horizons.

0-18 cm - Loamy sand 7.5 YR 4/2 (brown), weak fine sub-angular blocky structure, soft, very frequent fine and medium roots. Many pores, very good porosity, with a clear boundary.

18-53 cm - Sandy loam 10YR 7/6 (yellow), slightly moderate medium sub-angular blocky structure, slightly hard. Frequent fine and medium roots. Good porosity, diffuse boundary.

53-85 cm - Sandy clay 10 YR 8/4 (very pale brown), strong moderate medium sub-angular blocky structure, slightly hard. Frequent fine and medium roots, with few coarse one. Common pores, good porosity, clear boundary.

85-130+ cm - Sandy clay 10 YR 7/1 (light grey), moderate medium sub-angular blocky structure, slightly hard. Common fine and medium roots, with few coarse one. Common pores, good porosity.

Table 7.2. Soil chemical properties and particle size composition from each soil horizon (Table 7.1) from transect 1 in the PRF boundary on Maracá Island, Brazil. (a) Pit1= quadrat 1 (lower slope) of transect 1, (b) Pit2= plot 2 of PRFa, and (c) Pit3= quadrat 18 (plateau) of transect 1.

Horizon depth	pH	Loss. ign.	Ntotal	Ptotal	K+	Na+	Ca2+	Mg2+	total acidity	Al+++	H+	CEC	Mg/Ca	Base sat.	Clay	Silt	Sand
(cm)		(%)	mg/g	µg/g	mequiv.kg^{-1}									(%)	(%)	(%)	(%)
(a)																	
0-22	4.7	2.12	0.67	64.7	0.89	0.13	1.74	2.81	5.2	3.7	1.5	10.8	1.6	51.5	13	15	72
22-37	4.9	1.01	0.24	49.5	0.26	0.08	0.44	1.46	3.7	3.1	0.6	6.0	3.3	37.4	14	15	71
37-66	5.1	0.54	0.13	44.4	0.27	0.03	0.43	1.20	3.4	3.3	0.1	5.0	2.8	31.6	14	15	71
66-77	5.3	0.13	0.06	41.3	0.11	0.04	0.24	1.21	2.0	1.9	0.1	3.6	5.0	44.5	15	13	72
77-89	5.7	2.99	0.17	38.3	0.04	0.02	0.11	0.70	2.8	1.4	1.4	3.6	6.4	24.2	14	14	72
(b)																	
0-10	4.9	1.67	0.61	90.0	1.07	0.04	1.90	1.66	9.0	4.4	4.6	13.7	0.9	34.2	14	14	72
10-35	5.0	1.21	0.38	82.9	0.63	0.04	1.08	0.95	8.5	5.0	3.5	11.2	0.9	24.1	15	14	71
35-62	5.1	0.70	0.23	68.7	0.54	0.10	0.49	0.99	7.5	5.1	2.4	9.6	2.0	22.0	16	12	72
62-120	5.0	0.52	0.15	60.6	0.50	0.21	0.25	2.76	7.0	4.2	2.8	10.7	11.0	34.7	18	11	71
(c)																	
0-18	5.0	3.87	0.80	79.9	4.09	0.13	4.32	4.40	4.5	3.4	1.1	17.4	1.0	74.2	19	5	76
18-53	5.1	3.21	0.39	55.5	3.17	0.13	0.38	2.83	5.5	4.1	1.4	12.0	7.4	54.3	23	6	71
53-85	5.1	2.15	0.23	42.4	1.37	0.12	0.03	1.17	6.3	5.3	1.0	8.9	39.0	30.1	32	9	59
85-130	5.0	0.65	0.27	42.4	0.93	0.11	0.09	1.10	7.0	5.4	1.6	9.2	12.0	24.2	22	10	68

Table 7.3. Soil chemical properties from soil surface (0-10 cm) from each quadrat of the transect 1.

Quadrats	Loss-on-ign. (%)	pH	$P_{extr.}$ µg/g	Al3+ meq/100g	H+ meq/100g	K+ meq/kg	Ca2+ meq/kg	Mg2+ meq/kg	Mg/Ca
1	2.10	4.5	3.80	0.34	0.23	0.76	1.17	2.21	1.88
2	1.43	4.8	2.70	0.32	0.20	0.55	1.04	1.63	1.57
3	2.26	4.7	3.80	0.35	0.25	0.63	1.23	2.46	2.01
4	2.24	4.6	4.50	0.42	0.33	0.72	1.30	2.33	1.79
5	2.67	4.5	5.20	0.31	0.29	0.65	1.18	2.61	2.22
6	1.59	4.6	4.00	0.23	0.24	0.58	0.88	2.17	2.46
7	1.86	4.6	4.80	0.20	0.27	0.85	0.55	2.03	3.67
8	2.20	4.6	4.70	0.25	0.32	0.86	0.94	3.06	3.25
9	1.50	4.7	3.20	0.18	0.24	0.58	0.41	2.02	4.93
10	2.23	4.8	4.30	0.21	0.24	0.90	0.78	3.62	4.65
11	2.35	4.6	4.20	0.32	0.28	0.68	0.84	3.00	3.55
12	2.35	4.7	4.10	0.25	0.27	1.03	0.85	3.40	4.01
13	2.82	4.7	3.90	0.33	0.37	1.00	2.28	5.38	2.36
14	1.41	4.8	3.80	0.17	0.20	0.63	1.33	1.98	1.48
15	2.53	5.3	5.90	0.05	0.15	0.89	1.38	3.08	2.23
16	2.04	4.8	7.30	0.19	0.33	1.40	1.88	3.76	2.01
17	2.54	4.9	2.60	0.28	0.27	0.82	1.11	2.66	2.39
18	1.60	4.5	4.10	0.28	0.27	0.64	0.66	1.98	2.98

Table 7.4. Soil chemical properties from soil surface (0-10 cm) from each quadrat of the transect 2.

Quadrats	Loss-on-ign. (%)	pH	$P_{extr.}$ µg/g	Al3+ meq/100g	H+ meq/100g	K+ meq/kg	Ca2+ meq/kg	Mg2+ meq/kg	Mg/Ca
19	1.52	4.5	3.60	0.24	0.23	0.46	0.64	1.71	2.68
20	1.44	4.6	4.30	0.21	0.21	0.70	1.34	2.29	1.71
21	2.51	4.9	5.20	0.24	0.26	0.75	2.71	2.77	1.02
22	2.96	4.8	4.50	0.31	0.29	1.18	2.82	4.09	1.45
23	1.84	4.8	3.70	0.22	0.20	0.53	0.81	1.79	2.20
24	1.97	4.9	2.70	0.34	0.26	0.73	1.22	2.83	2.32
25	2.68	4.7	2.40	0.48	0.34	0.78	0.99	2.73	2.77
26	2.73	4.7	2.40	0.57	0.35	1.07	0.84	3.09	3.69
27	2.34	4.6	2.90	0.57	0.35	0.98	1.02	3.14	3.08
28	3.66	4.6	3.10	0.71	0.36	1.00	1.71	3.77	2.21
29	2.49	4.6	3.50	0.60	0.32	0.75	1.26	2.55	2.03
30	2.69	4.6	2.90	0.64	0.23	0.74	2.23	2.26	1.02
31	2.07	4.6	2.60	0.57	0.23	0.69	0.64	1.88	2.93
32	2.46	4.6	3.00	0.57	0.25	0.77	0.92	2.23	2.43
33	2.86	4.5	3.40	0.52	0.33	0.74	0.70	2.46	3.50
34	2.22	4.7	4.10	0.4	0.22	0.71	0.75	1.87	2.48
35	2.85	4.6	3.00	0.39	0.28	0.79	1.08	2.56	2.37
36	2.57	4.6	2.60	0.57	0.30	0.69	0.34	0.96	2.84

Table 7.5. Soil chemical properties from soil surface (0-10 cm) from each quadrat of the transect 3.

Quadrats	Loss-on-ign. (%)	pH	$P_{extr.}$ µg/g	Al3+ meq/100g	H+ meq/100g	K+ meq/kg	Ca2+ meq/kg	Mg2+ meq/kg	Mg/Ca
37	1.58	4.8	4.10	0.28	0.12	0.66	0.91	1.75	1.92
38	2.00	5.0	5.70	0.20	0.17	0.70	2.07	2.03	0.98
39	1.49	5.1	5.10	0.19	0.13	0.81	1.64	1.88	1.15
40	2.45	4.8	6.10	0.09	0.28	0.68	1.25	2.79	2.23
41	1.43	4.6	5.00	0.18	0.27	0.54	0.66	1.49	2.25
42	1.84	4.5	5.10	0.32	0.28	0.58	0.92	2.32	2.52
43	1.91	4.6	4.20	0.38	0.27	0.70	1.25	4.09	3.27
44	2.47	4.6	5.80	0.46	0.29	0.86	1.47	2.06	1.40
45	1.47	4.8	4.40	0.30	0.17	0.70	0.77	1.39	1.81
46	1.28	4.9	4.40	0.24	0.13	0.83	0.85	1.75	2.07
47	2.49	4.5	5.00	0.46	0.31	0.73	0.68	1.71	2.51
48	2.02	4.9	4.40	0.30	0.20	1.07	1.13	1.79	1.58
49	1.54	4.9	3.20	0.19	0.16	0.66	0.84	1.36	1.61
50	1.40	4.7	3.70	0.15	0.20	0.51	0.47	0.86	1.81
51	1.85	4.9	3.30	0.13	0.12	0.71	0.70	1.41	2.00
52	1.63	4.7	3.00	0.25	0.17	0.82	0.48	0.90	1.87
53	1.57	4.9	3.70	0.10	0.20	0.90	0.61	1.22	2.00
54	1.18	4.7	4.00	0.16	0.16	0.52	0.82	0.99	1.21

Table 7.6. Trees (≥ 10 cm dbh) density, maximum dbh, mean dbh and basal area for each transect studied on Maracá Island, RR, Brazil. Transects ranked by basal area.

	N (ha^{-1})	dbh max	dbh mean	BA (m^2ha^{-1})
Transect 1	511	77.7	25.4	35.7
Transect 3	431	108.2	25.5	31.6
Transect 2	478	69.1	22.5	25.1

Table 7.7. Family and species diversity and similarity amongst the three transects studied on Maracá Island, RR, Brazil. Nf= number of families, H'f= family Shannon diversity index, Nspp.= number of species, H'spp.= species Shannon diversity index, Even.= evenness.

	Richness and diversity				
	Nf	H'f	Nspp.	H'spp.	Even
Transect 1	21	2.41	35	2.86	0.81
Transect 2	23	2.45	37	2.98	0.83
Transect 3	24	2.49	28	2.99	0.82
	Similarity (Sϕrensen index)				
Transects	1 x 2		1 x 3	2 x 3	
Family	73%		84%	72%	
Species	34%		35%	35%	

between transects (Table 7.7).

Peltogyne was the most abundant tree species, with the highest values of basal area in all transects (Tables 7.8-7.10). As found for PRF plots, *Ecclinusa guianensis*, *Lecythis corrugata* and *Pradosia surinamensis* were always among the 10 most important species in the transects. The most important species in the FWP plots, *Licania kunthiana*, occurred only in transect 3 and was represented by only two individuals. Henceforth the above species will be referred to by their generic names only.

Peltogyne occurred with most individuals (seedlings, new established seedlings, saplings and trees) in the first twelve quadrats in all transects (Fig. 7.1-7.3). Although, mainly for transect 2, *Peltogyne* seedlings and saplings also occurred in high numbers in some plateau quadrats. *Pradosia*, although present in most quadrats of the transects, showed the same preference, as *Peltogyne*, for the lower-slope quadrats. It is noteworthy that the number of *Pradosia* saplings and trees seems be inversely related to the *Peltogyne* density in these quadrats (Figs. 7.1-7.3). *Ecclinusa*, *Lecythis* and *Licania* showed a strong preference for the middle slope and plateau quadrats (Figs. 7.1-7.3). All the seedlings (few individuals) of these three species occurred in the middle-slope and plateau quadrats.

FLORISTIC ORDINATION

The results of the DCA ordinations carried out for each transect, based on basal area and density data, were similar, with most quadrats from the lower slope in one extreme of axis I and most quadrats from the plateau in the other extreme (Fig. 7.4-7.6). The ordinations also showed that, in all transects, species such as *Peltogyne gracilipes*, *P. paniculata* and *Tabebuia uleana* were associated with the lower slope quadrats, while species such as *Duroia eriopila*, *Ecclinusa guianensis* and *Tetragastris*

Table 7.8. Species of trees ≥ 10 cm dbh occurring in the transect 1 (20 m x 180 m) on Maracá Island, RR, Brazil with number of individuals (N), total basal area (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI). Species ranked by CVI and total basal area.

Transect 1

Species	N	BA (m^2)	RD (%)	RDo (%)	CVI (%)
Peltogyne gracilipes	34	5.02	18.48	39.06	57.54
Pradosia surinamensis	22	2.28	11.96	17.77	29.73
Maximiliana maripa	22	1.24	11.96	9.65	21.61
Lecythis corrugata	21	0.77	11.41	5.98	17.39
Simarouba amara	4	0.84	2.17	6.57	8.75
Alseis longifolia	12	0.14	6.52	1.10	7.62
Ecclinusa guianensis	6	0.34	3.26	2.65	5.91
Tetragastris panamensis	6	0.24	3.26	1.87	5.13
Pouteria surumuensis	6	0.20	3.26	1.58	4.84
Himatanthus articulatus	6	0.10	3.26	0.74	4.00
Mauritia flexuosa	4	0.19	2.17	1.48	3.65
Crepidospermum goudotianum	5	0.06	2.72	0.50	3.22
Couepia paraensis	3	0.20	1.63	1.55	3.18
Couratari multiflora	1	0.26	0.54	2.05	2.59
Duroia eriopila	4	0.05	2.17	0.40	2.57
Brosimum guianensis	3	0.09	1.63	0.70	2.33
Drypetes variabilis	1	0.20	0.54	1.57	2.11
Lonchocarpus sp.	3	0.04	1.63	0.31	1.94
Gustavia augusta	2	0.08	1.09	0.60	1.68
Picramnia cf. spruceana	2	0.04	1.09	0.35	1.44
Inga sp.1	2	0.03	1.09	0.27	1.36
Tabebuia uleana	2	0.03	1.09	0.25	1.34
Cochlospermum orinocense	1	0.10	0.54	0.78	1.32
Licania apetala	1	0.07	0.54	0.55	1.09
Hymenaea courbaril	1	0.05	0.54	0.42	0.96
Eschweilera pedicellata	1	0.04	0.54	0.31	0.86
Exellondendron barbatum	1	0.03	0.54	0.25	0.79
Eugenia cupulata	1	0.02	0.54	0.18	0.72
Ryania speciosa	1	0.01	0.54	0.11	0.65
Guatteria schomburgkiana	1	0.01	0.54	0.08	0.62
Swartzia laurifolia	1	0.01	0.54	0.08	0.62
Vitex schomburgkiana	1	0.01	0.54	0.07	0.61
Inga bourgonii	1	0.01	0.54	0.07	0.61
Machaerium biovulatum	1	0.01	0.54	0.06	0.61
Lueheopis duckeana	1	0.01	0.54	0.06	0.61

Table 7.9. Species of trees ≥ 10 cm dbh occurring in the transect 2 (20 m x 180 m) on Maracá Island, RR, Brazil with number of individuals (N), total basal area (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI). Species ranked by CVI and total basal area.

Transect 2					
Species	N	BA (m^2)	RD (%)	RDo (%)	CVI (%)
Peltogyne gracilipes	23	3.15	13.37	34.81	48.18
Ecclinusa guianensis	25	1.09	14.53	12.11	26.64
Lecythis corrugata	24	0.95	13.95	10.57	24.52
Pradosia surinamensis	14	0.58	8.14	6.42	14.56
Maximiliana maripa	10	0.57	5.81	6.28	12.09
Tabebuia uleana	5	0.37	2.91	4.08	6.99
Alseis longifolia	9	0.12	5.23	1.35	6.58
Peltogyne paniculata	5	0.26	2.91	2.90	5.81
Chomelia barbellata	5	0.15	2.91	1.63	4.54
Tetragastris panamensis	4	0.19	2.33	2.14	4.47
Simarouba amara	3	0.18	1.74	1.95	3.70
Eschweilera pedicellata	2	0.18	1.16	2.04	3.20
Duroia eriopila	4	0.07	2.33	0.74	3.07
Enterolobium schomburgkii	3	0.12	1.74	1.30	3.04
Amaioua corymbosa	4	0.04	2.33	0.49	2.82
Couratari multiflora	1	0.18	0.58	1.98	2.56
Genipa americana	2	0.12	1.16	1.30	2.46
Couepia paraensis	3	0.06	1.74	0.66	2.40
Picramnia cf. spruceana	3	0.05	1.74	0.58	2.32
MTN 2791	1	0.14	0.58	1.60	2.19
Guapira sp.	2	0.03	1.16	0.37	1.54
Himatanthus articulatus	2	0.03	1.16	0.36	1.52
Crepidospermum goudotianum	2	0.03	1.16	0.31	1.47
Maytenus guianensis	2	0.02	1.16	0.27	1.43
Inga sp.1	1	0.07	0.58	0.79	1.38
Drypetes variabilis	2	0.02	1.16	0.19	1.35
MTN 2847	1	0.05	0.58	0.59	1.17
Guatteria schomburgkiana	1	0.04	0.58	0.42	1.00
Bauhinia ungulata	1	0.03	0.58	0.30	0.88
Aniba hostmanniana	1	0.02	0.58	0.25	0.83
Apeiba schomburgkii	1	0.02	0.58	0.25	0.83
Oenocarpus bacaba	1	0.02	0.58	0.24	0.82
MTN 2864	1	0.02	0.58	0.24	0.82
Inga alba	1	0.01	0.58	0.16	0.74
MTN 2876	1	0.01	0.58	0.13	0.71
Lueheopis duckeana	1	0.01	0.58	0.11	0.69
Machaerium sp.	1	0.01	0.58	0.11	0.69

Table 7.10. Species of trees ≥ 10 cm dbh occurring in the transect 3 (20 m x 180 m) on Maracá Island, RR, Brazil with number of individuals (N), total basal area (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI). Species ranked by CVI and total basal area.

Transect 3 Species	N	BA (m^2)	RD (%)	RDo (%)	CVI (%)
Peltogyne gracilipes	32	4.44	20.65	39.01	59.66
Pradosia surinamensis	11	1.69	7.10	14.83	21.93
Maximiliana maripa	17	1.11	10.97	9.74	20.71
Ecclinusa guianensis	15	0.60	9.68	5.31	14.99
Lecythis corrugata	12	0.64	7.74	5.60	13.34
Simarouba amara	6	0.60	3.87	5.28	9.15
Vitex schomburgkiana	4	0.37	2.58	3.29	5.87
Tabebuia uleana	6	0.18	3.87	1.59	5.46
Peltogyne paniculata	4	0.13	2.58	1.10	3.68
Protium crenatum	2	0.2	1.29	2.36	3.65
Alseis longifolia	4	0.07	2.58	0.62	3.20
Licania kunthiana	2	0.19	1.29	1.66	2.95
Duroia eriopila	3	0.09	1.94	0.82	2.76
Himatanthus articulatus	3	0.09	1.94	0.77	2.70
Pouteria hispida	3	0.06	1.94	0.51	2.45
Picramnia cf. spruceana	3	0.05	1.94	0.41	2.34
Pouteria surumuensis	2	0.10	1.29	0.92	2.21
Pouteria reticulata	2	0.10	1.29	0.87	2.16
Tetragastris panamensis	2	0.06	1.29	0.49	1.78
Eugenia cupulata	2	0.04	1.29	0.39	1.68
Agonandra silvatica	1	0.11	0.65	0.96	1.60
Spondias mombin	1	0.11	0.65	0.93	1.57
Guatteria schomburgkiana	2	0.03	1.29	0.27	1.56
Quiina cf. rhytidopus	2	0.02	1.29	0.17	1.46
Inga sp.	1	0.04	0.65	0.31	0.96
Eugenia sp.	1	0.03	0.65	0.26	0.91
Xanthoxylum aff. rigidum	1	0.02	0.65	0.21	0.86
Ficus sp.	1	0.02	0.65	0.19	0.83
Chomelia barbellata	1	0.02	0.65	0.17	0.81
Drypetes variabilis	1	0.02	0.65	0.14	0.79
Lueheopis duckeana	1	0.02	0.65	0.13	0.77
Machaerium sp.	1	0.01	0.65	0.12	0.77
Maytenus guianensis	1	0.01	0.65	0.11	0.76
Cecropia sp.	1	0.01	0.65	0.11	0.75
Lonchocarpus sp.	1	0.01	0.65	0.09	0.74
Cheiloclinum cognatum	1	0.01	0.65	0.09	0.73
Crepidospermum goudotianum	1	0.01	0.65	0.08	0.73
Faramea crassiloba	1	0.01	0.65	0.08	0.73

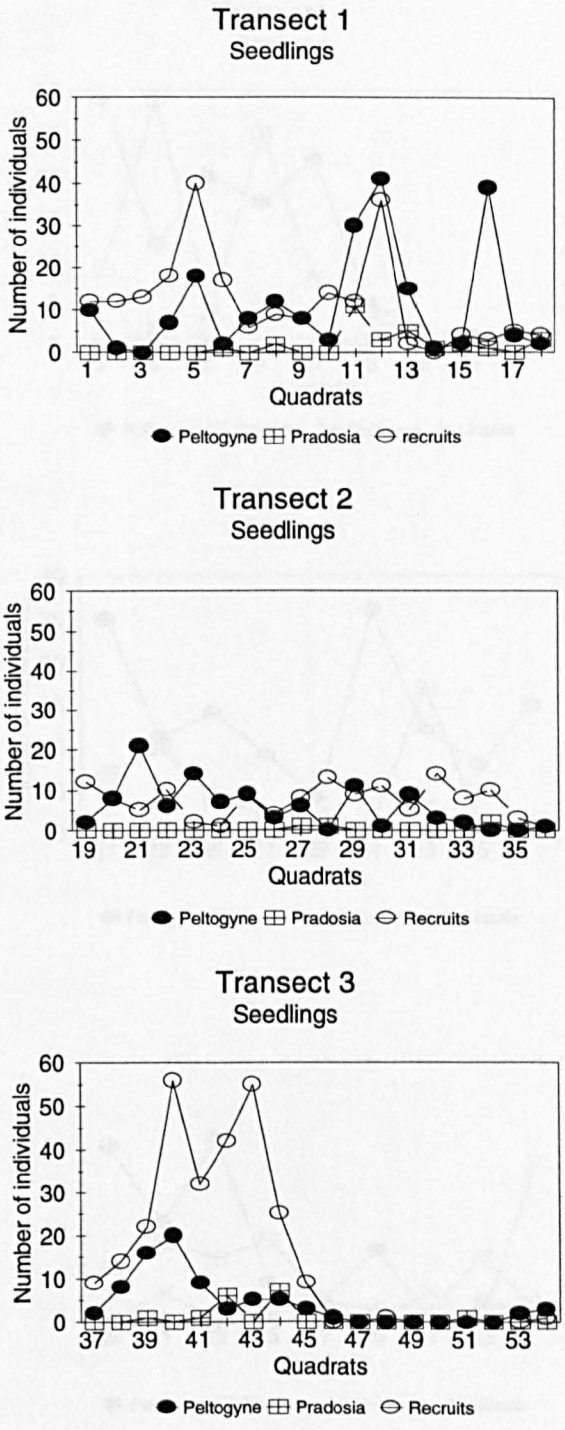


Figure 7.1. Number of seedlings of Peltogyne and Pradosia and Peltogyne recruits per quadrat in each study transect.

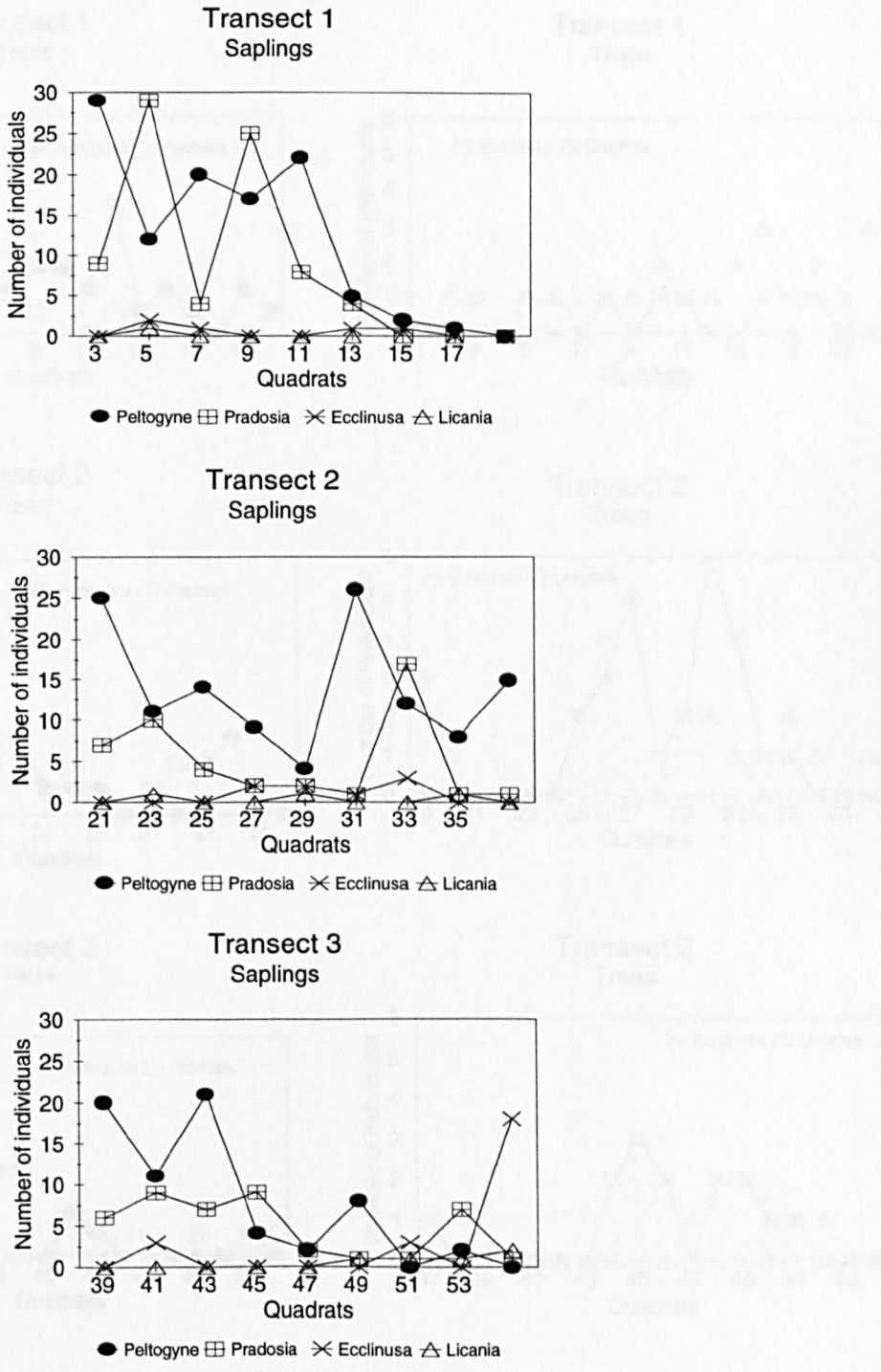


Figure 7.2. Number of saplings of four important species per quadrat in each study transect.

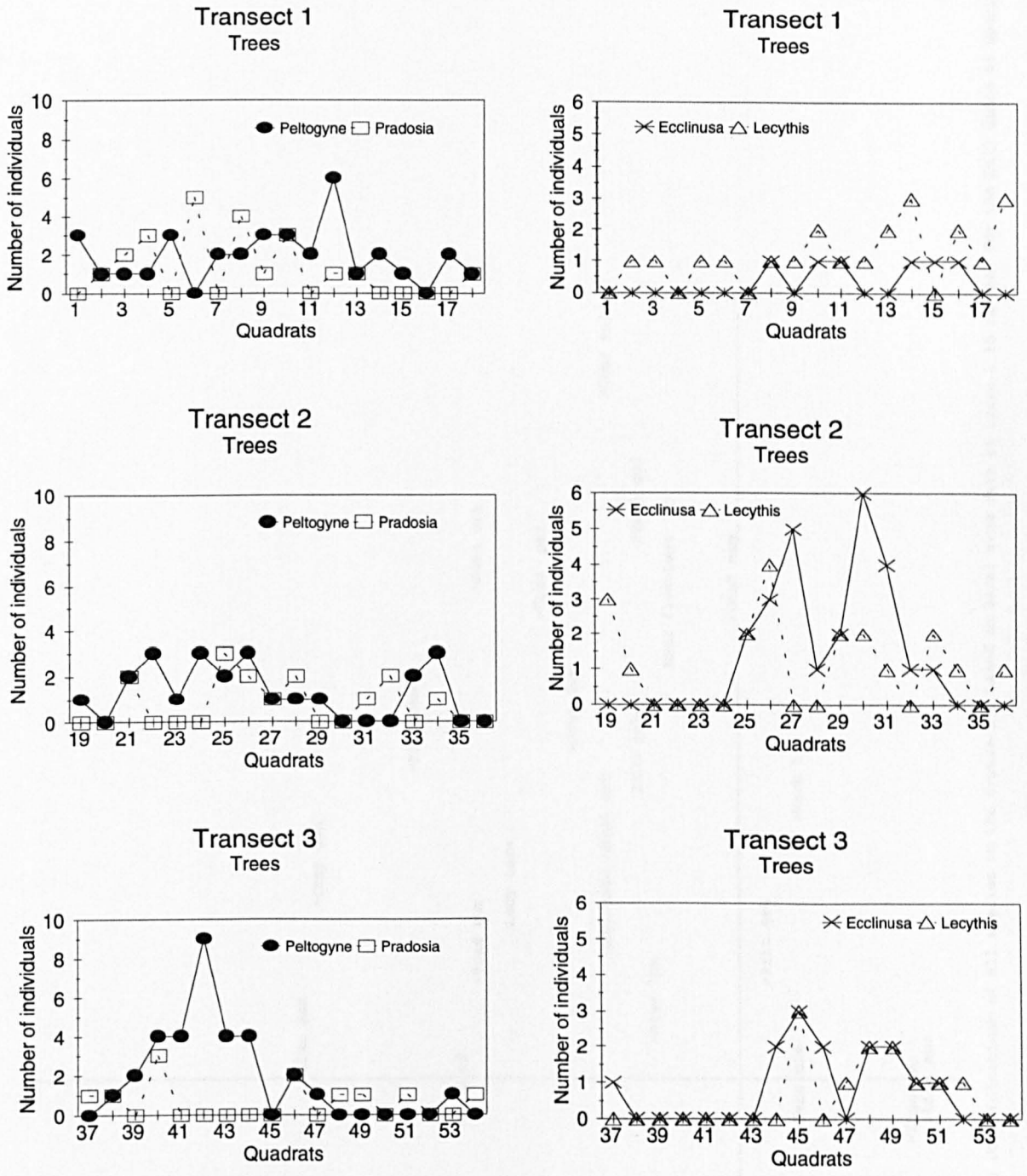


Figure 7.3. Number of trees of the four most important species per quadrat in each study transect.

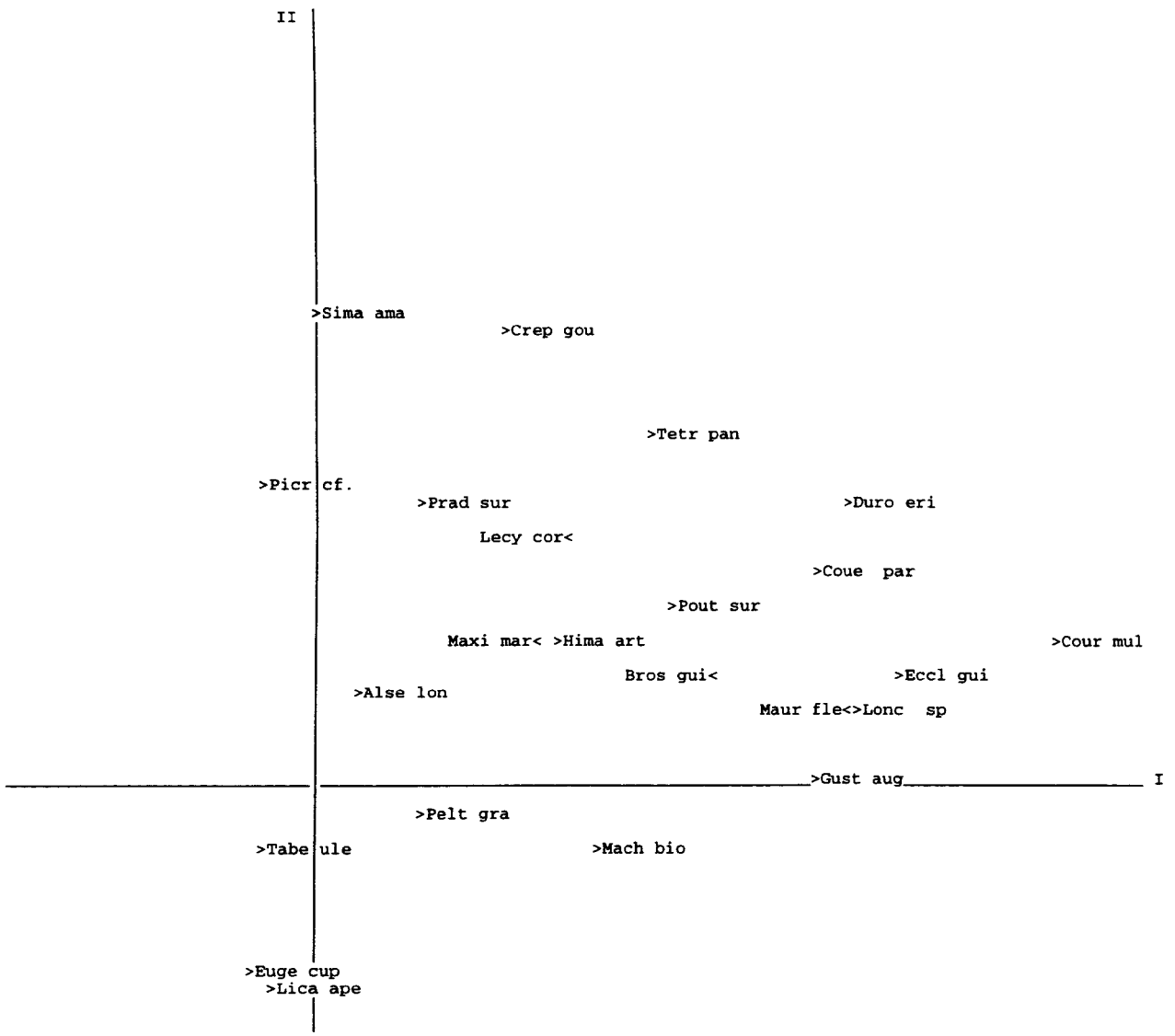


Fig. 7.4. (a) DCA ordinations of all species in the transect 1 based on basal area data of trees ≥ 10 cm dbh. For the full names of species see Appendix 2.

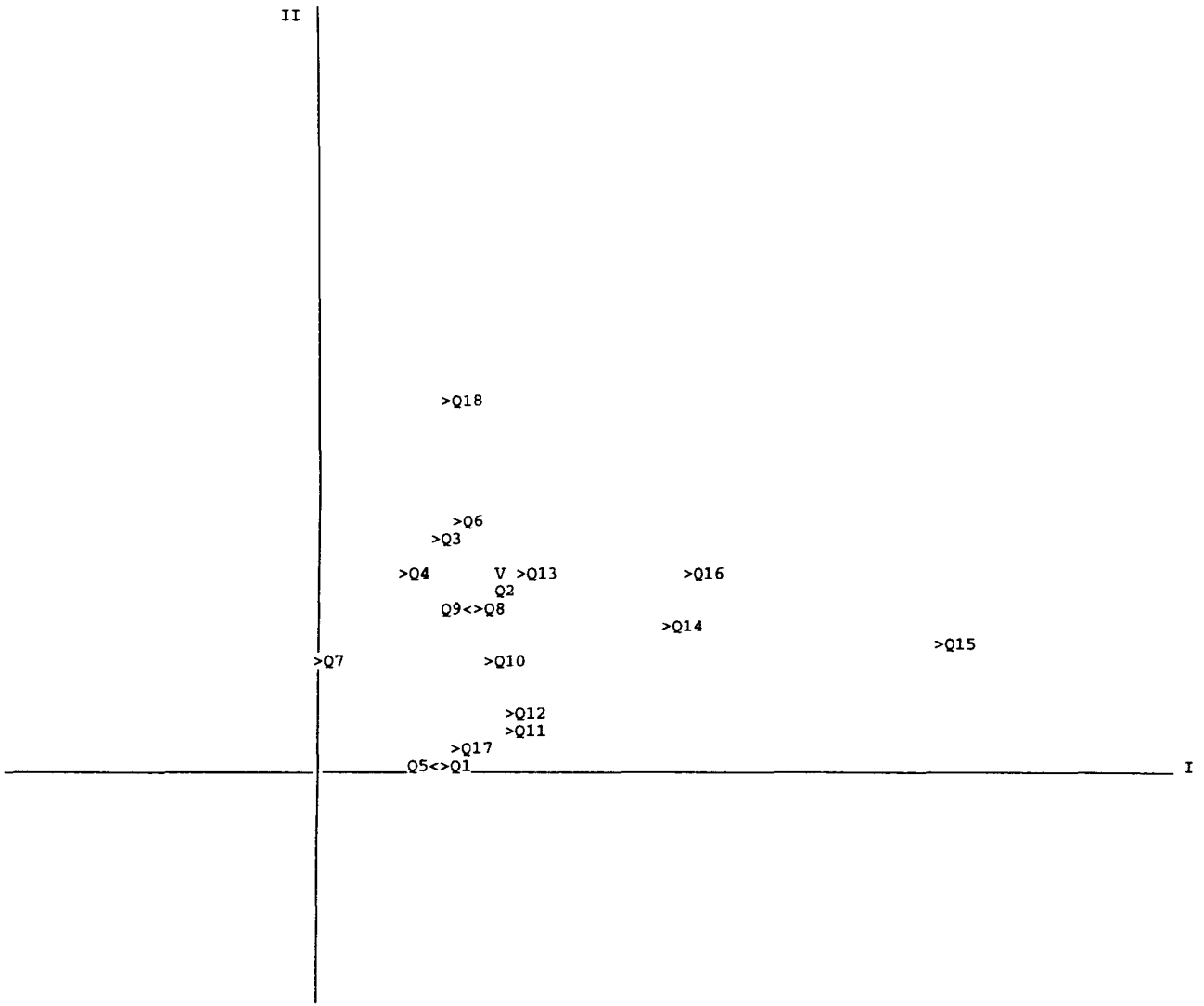


Fig. 7.4. (b) DCA ordinations of 18 quadrats in the transect 1 based on basal area data of trees ≥ 10 cm dbh.

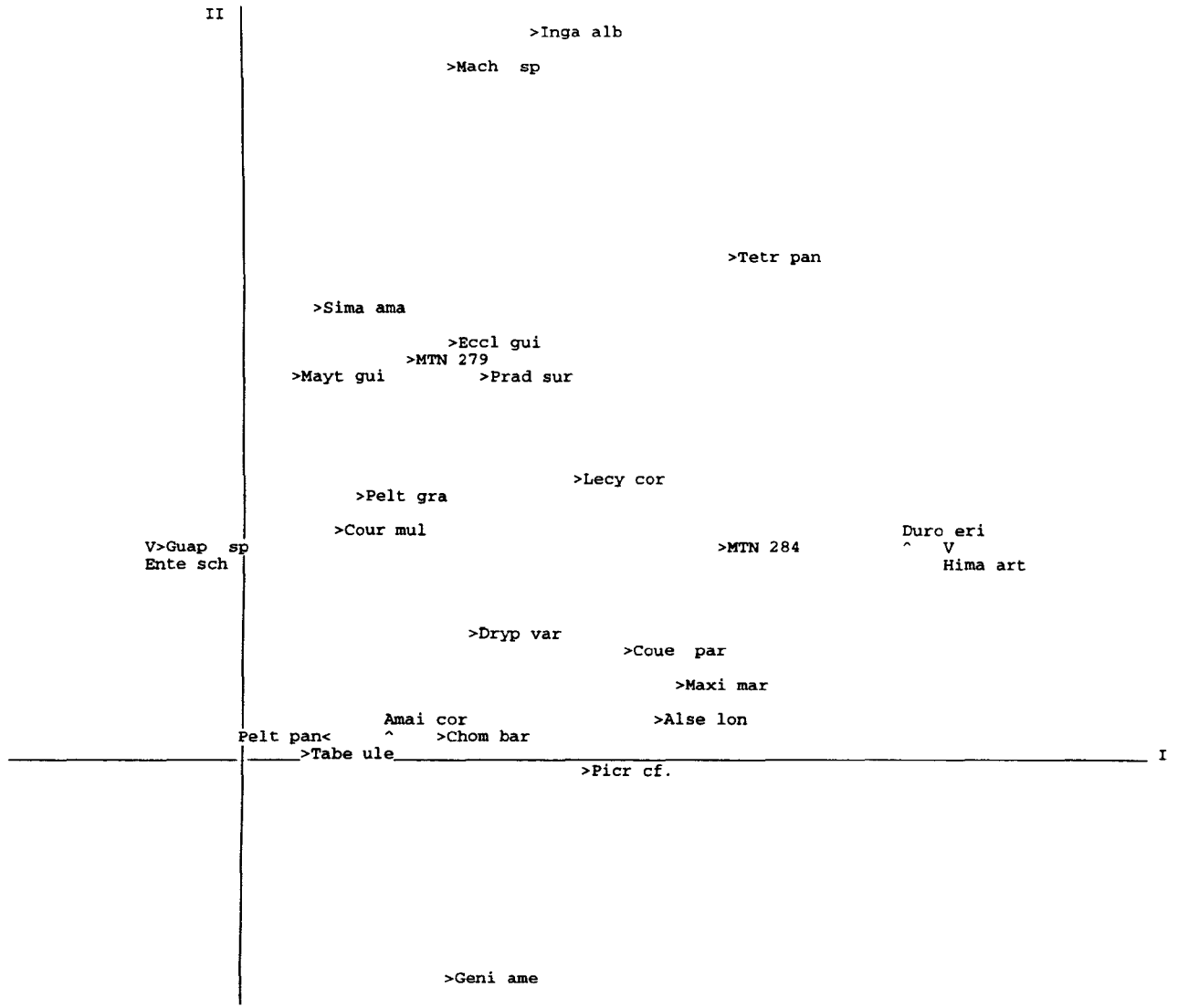


Fig. 7.5. (a) DCA ordinations of all species in the transect 2 based on basal area data of trees ≥ 10 cm dbh. For the full names of species see Appendix 2.

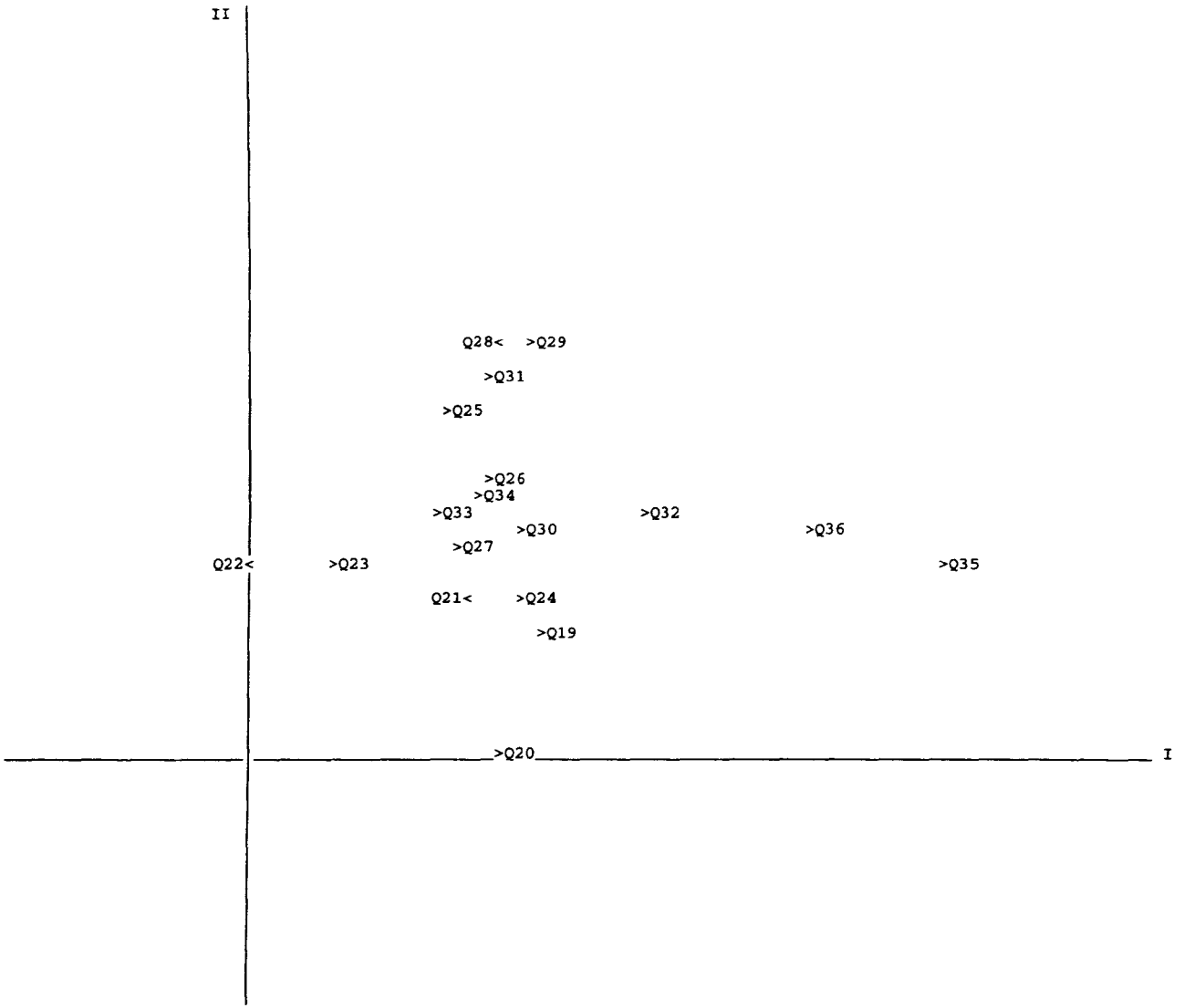


Fig. 7.5. (b) DCA ordinations of 18 quadrats in the transect 2 based on basal area data of trees ≥ 10 cm dbh.

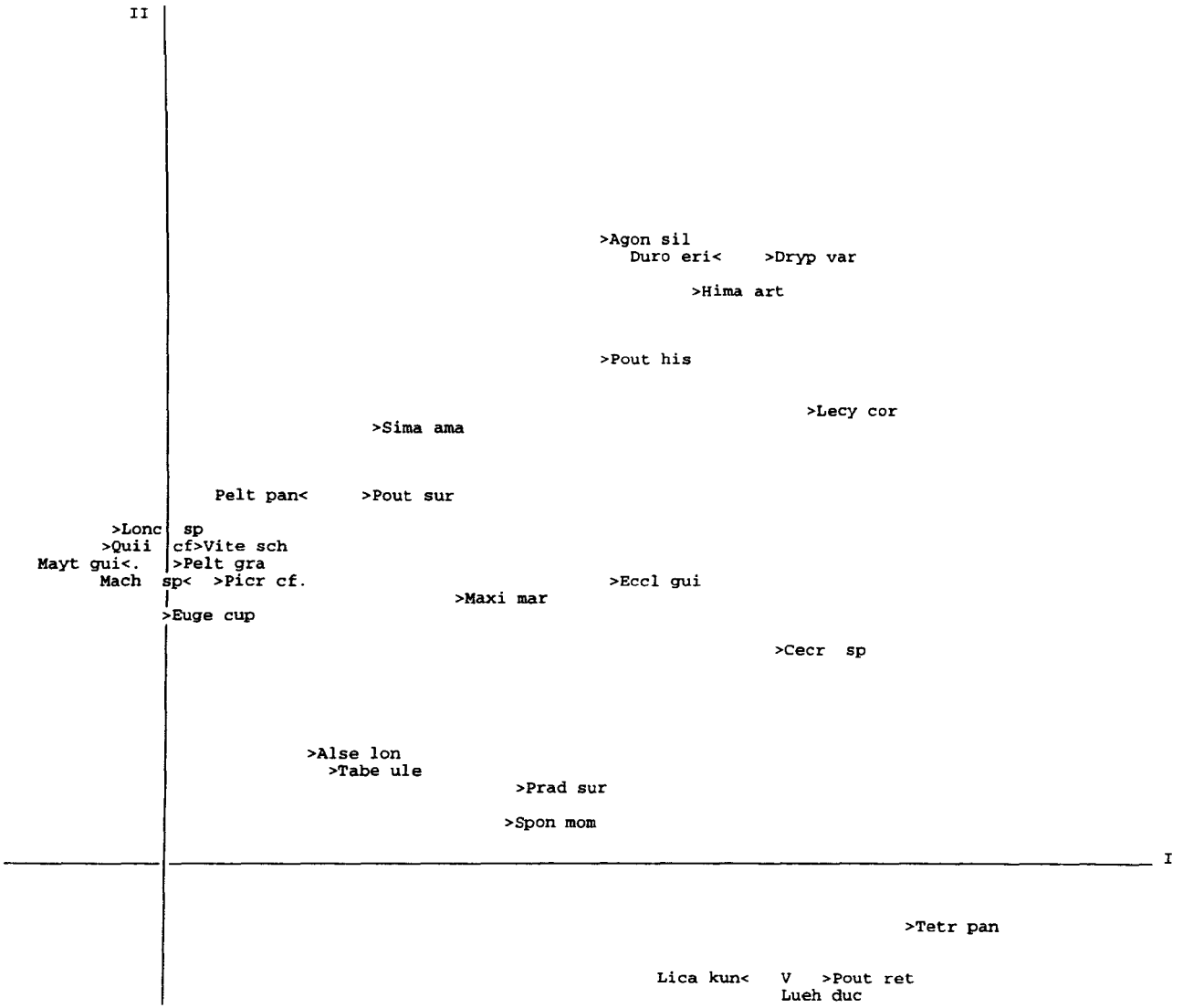


Fig. 7.6. (a) DCA ordinations of all species in the transect 3 based on basal area data of trees ≥ 10 cm dbh. For the full names of species see Appendix 2.

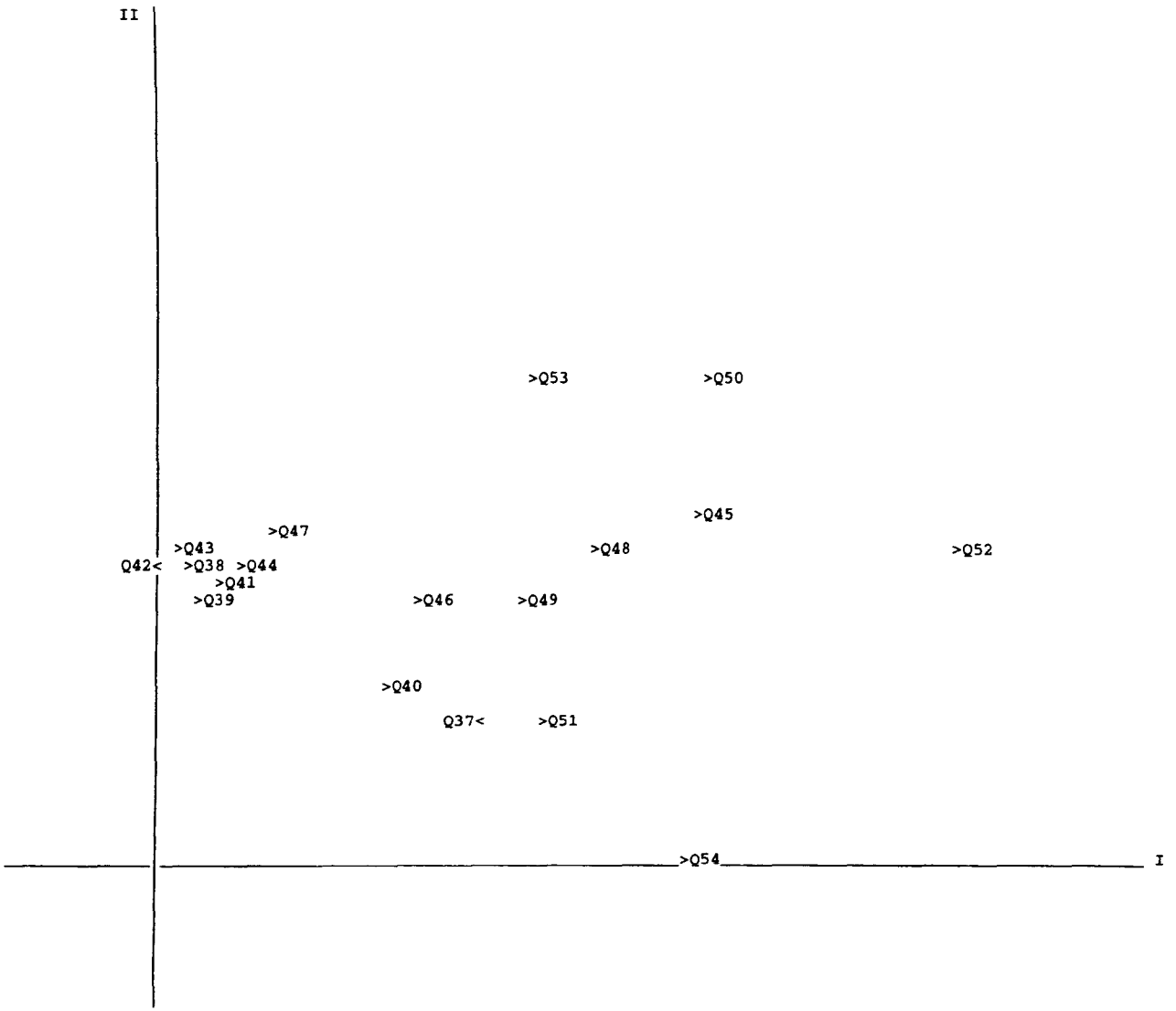


Fig. 7.6. (b) DCA ordinations of 18 quadrats in the transect 3 based on basal area data of trees ≥ 10 cm dbh.

panamensis were associated with the plateau quadrats.

The ordinations of the quadrats and species by the DCCA analyses for each transect were similar to those produced by the DCA analyses. The eigenvalues and cumulative percentage variance of species-environment relationship for each analysis are shown in Table 7.11. The environmental variables were apparently insufficient to explain most of the floristic variation among the quadrats. The Monte Carlo test applied for the first canonical axis showed that species were not significantly correlated with environmental variables supplied ($p>0.05$), except for the DCCA analysis for basal area data of transect 1 ($p= 0.04$). This analysis showed that pH was positively correlated with axis I ($r= 0.84$) and Al negatively correlated ($r= - 0.65$). The variable that showed the strongest correlation with axis II was loss-on-ignition ($r= - 0.57$). However, a significant positive correlation ($r_s= 0.47$, $n= 54$, $p\leq 0.001$) was found between the number of *Peltogyne* trees and the Mg concentration in the surface soils of the three study transects.

FLORISTIC CLASSIFICATION OF THE TRANSECTS

The results of the TWINSPAN analyses applied on the quadrats of all transects considering the basal area and the density data for trees ≥ 10 cm dbh are shown in Tables 7.12 and 7.13. Only one distinct division was considered ecologically meaningful for quadrat groups from each analysis, since TWINSPAN divides poorly on a short gradient. A final quadrat group was determined using the results of both analyses. Quadrats number 2, 25 and 45 (group 2) and 17 and 34 (group 1) although split in these groups in both analyses were not located in these groups in the final quadrat group because they were considered to be outliers. Therefore, group 1 was formed by quadrats 1 to 12 (transect 1), 19 to 28 (transect 2) and 37 to 47 (transect 3) and group 2 by quadrats 13 to 18 (transect 1), 29-36 (transect

Table 7.11. The eigenvalues and cumulative percentage variance of species data (CPVS) of the DCA and CPVS and species-environmental relations (CPVS-E) of the DCCA analyses for each transect based on basal area data for trees ≥ 10 cm dbh.

	DCA				DCCA			
Axis	I	II	III	IV	I	II	III	IV
Transect 1								
Eigenvalues	0.63	0.41	0.21	0.08	0.58	0.29	0.10	0.05
CPVS	21.6	35.7	42.9	45.5	19.7	29.5	32.8	34.5
CVPS-E					27.4	47.5	0	0
Transect 2								
Eigenvalues	0.85	0.49	0.26	0.14	0.62	0.46	0.14	0.10
CPVS	19.8	31.3	37.4	40.6	14.4	25.2	28.6	30.8
CVPS-E					20.3	40.5	0	0
Transect 3								
Eigenvalues	0.79	0.45	0.20	0.10	0.69	0.17	0.09	0.04
CVPS	19.2	30.4	35.2	37.8	16.8	20.9	23.2	24.1
CVPS-E					31.6	42.5	0	0

Table 7.12. Twinspan two-way table based on the basal area data for trees ≥ 10 cm dbh from three transects (transect 1= plots 1-18, transect 2= plots 19-36 and transect 3= plots 37-54) located at the PRF boundary on Maracá Island, Roraima, Brazil. For the full name of the species see Appendix 2.

PLOTS

```
                 22224234  1144 2344 4   11223111234233411513553  34553
SPECIES          02374191159723748764038901684238519903545266032267814 5

 56 MTN   279  -------------------------3--------------------------  000000
 64 Mach  bio  ----------------------------1------------------------  000000
 66 MTN   286  ----------------------------1------------------------  000000
 18 Euge   sp  -----------------1----------------------------------  000001
 49 Xant  aff  -----------------1----------------------------------  000001
 23 Fara  cra  ----------------1-----------------------------------  00001
 38 Inga   sp  ----------------1-----------------------------------  00001
 41 Hyme  cou  -------------2--------------------------------------  00001
 62 Swar  lau  -------------1--------------------------------------  00001
  9 Sima  ama  -2-----------3-133-141---22--4--3----------1--------  0001
 15 Vite  sch  ----------------421-----------1----------------------  0001
 28 Dryp  var  --------------41--------------------1-------1--------  0001
 39 Gust  aug  ----------------------------2----------1-------------  0001
 45 Mayt  gui  --1-1-----------------------------1------------------  00100
 11 Pelt  pan  331--1-1--1--1----2----------------------------------  001010
 14 Apei  sch  -1---------------------------------------------------  001010
 16 Ente  sch  -31--------------------------------------------------  001010
 21 Euge  cup  ------11-1-------------------------------------------  001010
 46 Lica  ape  --------2--------------------------------------------  001010
 48 Quii   cf  ------------11-------------------------------------  001010
 50 Geni  ame  3----------------------------------------------------  001010
 51 Bauh  ung  -1---------------------------------------------------  001010
 65 Guap   sp  -11--------------------------------------------------  001010
  6 Chom  bar  2--1------1----11---------1---------------------------  001011
 22 Mach   sp  -------1--------------------1-------------------------  001011
  1 Pelt  gra  -414535555355343541334324444443 12--4-4-21----1-1------  0011
  5 Tabe  ule  12-4-2221----------1------------------1----------2--1-  0011
 17 Picr  cf.  1--11--1-----------111-----------------------1-------  0011
  7 Alse  lon  1----12-121---------1--------1-1-----1------1--2-1111--  01
  8 Pout  sur  -------2-------------2--3--------------11---------2---  01
 10 Maxi  mar  2-2--2223-42--22223-3322-32-22---------2--3--3-4334331  01
  2 Prad  sur  ---1-1---1------1-4443434-221344234-----------4344341-  100
 54 Maur  fle  ------------------------1---2----------2-2-----------  100
  4 Lecy  cor  2--1-----221---1-1---121123331341122332 3-3122--11-41--  1010
 19 Lonc   sp  -----------1-1----------------1---------1-------------  1010
 33 Amai  cor  1--1-------------------------------11----------------  1010
 53 Bros  gui  -----------1---------1----------------2--------------  1010
  3 Eccl  gui  ---31------------11---1-1131----233242223-1-1-1--233--  1011
 31 Guat  sch  ----------------------------1----------1-1------------  1011
 35 Cour  mul  -------------------------------------3--4-------------  110000
 55 Inga  alb  ----------------------------------1-----------------  110000
 60 Cecr   sp  ---------------------------------------1--------------  110000
 37 Chei  cog  ----------------------------------------1------------  110001
 61 Prot  cre  ----------------------------------------4------------  110001
 29 Pout  his  ---------------------------------2----------1--------  11001
 36 Lica  min  ------------------------------------1-----------------  11001
 63 Inga  bou  ---------------------------------1--------------------  11001
 24 Coue  par  ---------------2--------------3---------1-3---1-------  1101
 30 Crep  gou  --------------1--------------11----------11-------1--  1101
 34 Tetr  pan  -----------1---------------1---3---1---1-133--1-----1-  1101
 40 Esch  ped  ------------------------------------2-------------3  1101
 27 Lueh  duc  ----------------------------------------1---1--------1-  111000
 20 Duro  eri  --------------------------------1---------1-112111-----1  111001
 32 Oeno  bac  ------------------------------------------1----------  111001
 42 Agon  sil  ------------------------------------------3---------  111001
 43 Inga  spl  --------------------------------1----------------------2  111001
 44 Anib  hos  ------------------------------------------1----------  111001
 26 Pout  ret  ------------------------------------------1----------3-  111010
 58 MTN   287  ------------------------------------------------------1  111010
 12 Ficu   sp  ----------------------------------------------------1--  111011
 25 Lica  kun  ------------------------------------------------23-----  111011
 47 Ryan  spe  ------------------------------------------------1------  111011
 52 Coch  ori  ------------------------------------------------3------  111011
 57 MTN   284  ----------------------------------------------2--------  111011
 59 Spon  mom  ------------------------------------------------3----  111011
 13 Hima  art  --------1--------------11-----------------1111-1--2--1  1111

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                      000000111    011111100001011110000 01      0000001
                      000111        001111          00001      011111
```

Table 7.13. Twinspan two-way table based on the density data for trees ≥ 10 cm dbh from three transects (transect 1= plots 1-18, transect 2= plots 19-36 and transect 3= plots 37-54) located at the PRF boundary on Maracá Island, Roraima, Brazil. For the full name of the species see Appendix 2.

PLOTS

```
                2244 1441234    14 233  32233422341122414511355l3 3551
SPECIES         231472237486463810117959407019563504897981382246625035

 15 Vite  sch  ----------21-------------------------1---1----------  1111
  7 Alse  lon  ------------22----11114-12-2----------1113-1---1-----  1111
  2 Prad  sur  -----1----123424-3-21-111-1-1132--2-2---11112-1--1----  1111
 10 Maxi  mar  -11-11--1112-221224121-111-----1---1--1332----12-41-1-  1110
  9 Sima  ama  1---1-----11--11-1------1----1------1-1----1--------1-  1110
 17 Picr  cf.  --11--------1-1--1-------11-----------------1---------  110
  5 Tabe  ule  2-2---------1-----1111---11------1------------1-------  110
 66 MTN   286  ------------------------1-----------------------------  101111
 59 Spon  mom  --------------------1-------------------------------  101111
 50 Geni  ame  -------------------------2-------------------------  101111
 49 Xant  aff  -----------1---------------------------------------  101111
 46 Lica  ape  ------------------1---------------------------------  101111
 38 Inga   sp  ----------1---------------------------------------  101111
 23 Fara  cra  ----------1---------------------------------------  101111
 18 Euge   sp  ----------1---------------------------------------  101111
 21 Euge  cup  --1-----------------11-----------------------------  101110
 65 Guap   sp  11------------------------------------------------  101101
 64 Mach  bio  -----1---------------------------------------------  101101
 62 Swar  lau  ----1----------------------------------------------  101101
 51 Bauh  ung  1--------------------------------------------------  101101
 48 Quii   cf  ------11-------------------------------------------  101101
 41 Hyme  cou  ----1----------------------------------------------  101101
 16 Ente  sch  21-------------------------------------------------  101101
 14 Apei  sch  1--------------------------------------------------  101101
 11 Pelt  pan  111----1---2-------1-----1------------1------------  101100
 53 Bros  gui  --------1-----1-----------------1-----------------  1010
 45 Mayt  gui  -1-1-------------------------1----------------------  1010
  1 Pelt  gra  3144255423121-122432-2333-1---232-321111--11-----1--11  1010
 54 Maur  fle  -----1----------1-----------------------------1-----1  100
 39 Gust  aug  -----1-------------------------------------------1  100
 28 Dryp  var  ----1----1-----------------1-----------------------1--  100
 19 Lonc   sp  -------11-----------------------------------1----------1  100
 22 Mach   sp  --1-------------------------------1-----------------  011
  6 Chom  bar  ---------11--------------11----1-------1-------------  011
  8 Pout  sur  --1----------2-------------------11----1-----------2  0101
 33 Amai  cor  -------------------------111----1-------------------  0100
 31 Guat  sch  ------------------------1----------1---------2-------  0100
  4 Lecy  cor  -----1--11---1111-----11111212242323221321 23-2-221-1--  0100
  3 Eccl  gui  ---2-------2---11---1-----4542231311121-21--1--1---1-1  0100
 60 Cecr   sp  --------------------------------1-------------------  001111
 56 MTN   279  --------------------------------1-------------------  001111
 63 Inga  bou  ------------------------------------------1---------  001110
 57 MTN   284  ----------------------------------------------1-------  001110
 55 Inga  alb  ---------------------------------------1--------------  001110
 36 Lica  min  ----------------------------------------------1---------  001110
 12 Ficu   sp  ---------------------------------------------1----------  001110
 61 Prot  cre  ----------------------------------------------2-------  00110
 37 Chei  cog  ----------------------------------------------1-------  00110
 26 Pout  ret  ----------------------------------------------11------  00110
 25 Lica  kun  ----------------------------------------1----1-------  00110
 43 Inga  spl  ------------------------------------------2-------1---  0010
 34 Tetr  pan  --------1-------------------------111-----211121-----  0010
 29 Pout  his  ----------------------------2----------------------1-  0010
 27 Lueh  duc  ---------------------------------1----------1-1-----  0010
 35 Cour  mul  ------------------------------1--------------------1  00011
 30 Crep  gou  ----1-----------------------------------112---12-----  00011
 58 MTN   287  -------------------------------------------------1---  000101
 52 Coch  ori  ------------------------------------------------1----  000101
 47 Ryan  spe  ------------------------------------------------1----  000101
 44 Anib  hos  -----------------------------------------------1-----  000101
 42 Agon  sil  -------------------------------------------------1-  000101
 40 Esch  ped  ---------------------------------1--------------2---  000101
 32 Oeno  bac  ------------------------------------------------1-----  000101
 20 Duro  eri  ---------------------------------------11--1112211  000101
 13 Hima  art  ----------------1----1----------1-----1------112111-  000100
 24 Coue  par  ---------2---------------------------1-1--1-----1  0000

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               00000000011111111111111110000000000000000000001111111
               00001111100111111111111111000000000000000000000110000001
                   011111  000000000000010000000011111111111  001111
                    00011  0000001111111 0001111100000000111
                           0011110000111    0111100000111
```

2) and 48 to 54 (transect 3) (Table 7.14).

The soil and floristic data were reanalysed based on these two groups.

Soil data

The soil data analyses showed that there is no statistically significant difference in soil properties between soils from group 1 and group 2 (Table 7.15), with only magnesium tending to be higher in group 1 (t test, p= 0.07).

Structural and floristic data

The structural data of the quadrat groups (Table 7.16) were similar, with both quadrat groups showing values of number of tree density, mean dbh, and basal area in the ranges found for PRF and PPF plots (Chapter 4, Table 4.3).

The diameter distribution patterns of some of the most important species (*Ecclinusa, Lecythis, Peltogyne* and *Pradosia*) in the quadrat groups showed a reversed-J shape curve (Fig. 7.7). All species had a high density of stems in the smallest dbh classes (10-30 cm). Within-species comparison, however, showed that there were differences in the diameter distribution between quadrat groups for *Ecclinusa* and *Lecythis*, which had 70% of their trees in the smallest dbh class (10-20 cm) in quadrat group 1, while in quadrat group 2 the values for this dbh class were 21.7% (*Ecclinusa*) and 37.9% (*Lecythis*). Both these species had more trees in quadrat group 2. For *Peltogyne* and *Pradosia* there was a reduction in the number of trees per hectare

Table 7.14. Quadrat groups (group 1 and group 2) determined after the TWINSPAN analyses for density and basal area data. Plots in bold are from group 2.

Transect 1	Transect 2	Transect 3
1	19	37
2	20	38
3	21	39
4	22	40
5	23	41
6	24	42
7	**25**	43
8	26	44
9	27	**45**
10	28	46
11	**29**	47
12	**30**	**48**
13	**31**	**49**
14	**32**	**50**
15	**33**	**51**
16	34	**52**
17	**35**	**53**
18	**36**	**54**

Table 7.15. Soil chemical properties and particle size composition from surface soil (0-10 cm) from 34 plots (group 1) and 20 plots (group 2) of the three transects on Maracá Island, Roraima, Brazil.

Plots	Loss. Ign. (%)	pH	$P_{extr.}$ µg/g	K	Ca	Mg	H^+	Al^{3+}	Sand (%)	Silt (%)	Clay (%)
				mequiv.kg^{-1}							
Group1	2.09	4.7	0.42	0.75	1.14	2.49	2.58	3.14	12.0	7.0	81.7
Group2	2.11	4.7	0.37	0.78	1.01	2.39	2.39	3.26	14.3	4.7	81.0

Table 7.16. Size, tree (≥ 10 cm dbh) density, maximum dbh, mean dbh and basal area for each quadrat group of the study transects on Maracá Island, RR, Brazil.

Quadrat groups	Size (ha)	N (ha^{-1})	dbh max (cm)	dbh mean (cm)	BA (m^2ha^{-1})
Group 1	0.66	479	108.2	24.7	32.3
Group 2	0.42	464	75.7	24.1	28.4

Table 7.17. Family and species diversity and similarity of the two quadrat groups of the study transects on Maracá Island, RR, Brazil. Nf= number of families, H'f= family Shannon diversity index, Nspp.= number of species, H'spp.= species Shannon diversity index, Even.= evenness.

Quadrat groups	Richness and diversity				
	Nf	H'f	Nspp.	H'spp.	Even
Group 1	25	2.33	46	2.82	0.74
Group 2	24	2.54	42	3.17	0.85

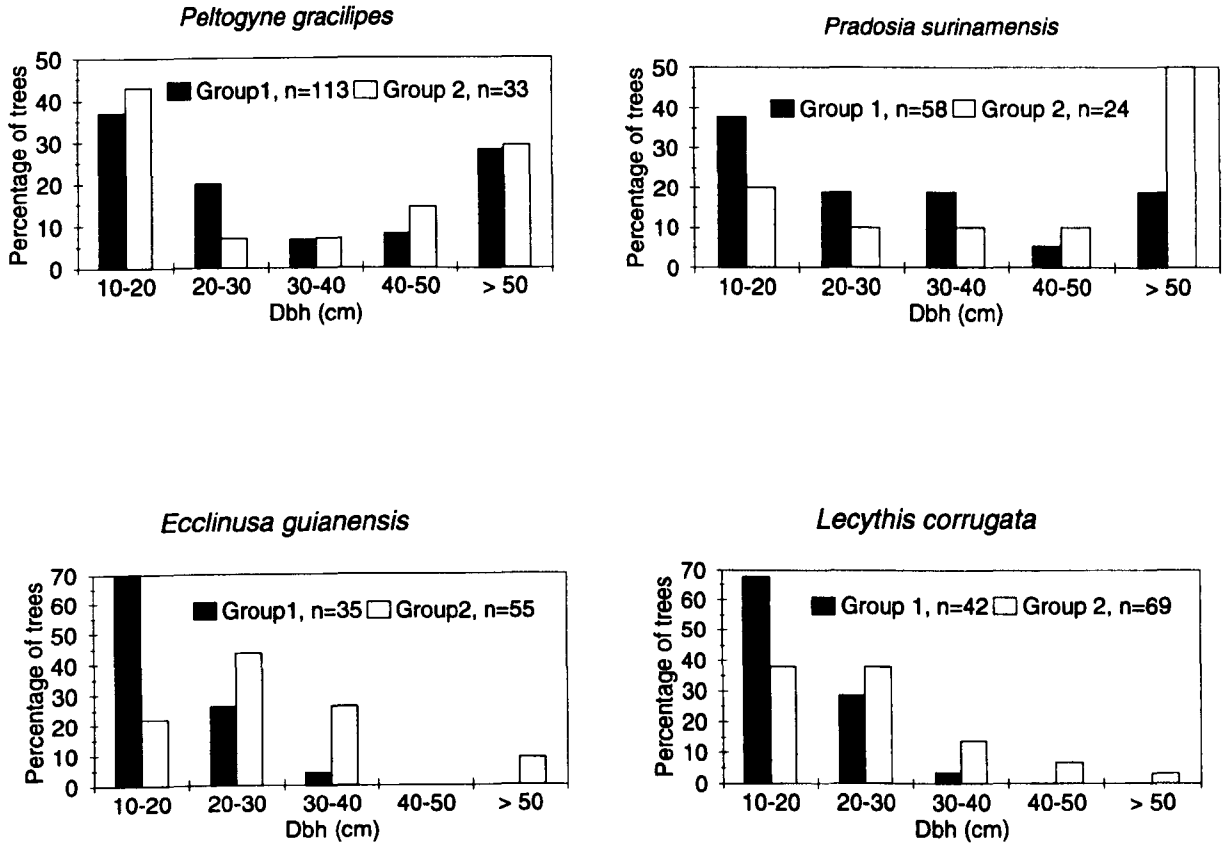

Figure 7.7. Distribution of diameter of trees >= 10 cm dbh of four species in each transect quadrat group. n= number of trees per hectare.

from group 1 (113, *Peltogyne*, and 58, *Pradosia*) to group 2 (33, *Peltogyne*, and 24, *Pradosia*). However, the diameter distribution patterns were similar between groups in both species.

The number of families were similar between the two quadrat groups. Although quadrat group 1 had more species than quadrat group 2, its diversity and evenness values were lower, reflecting the increasing dominance of *Peltogyne* (Table 7.17). The list of species of trees ≥ 10 cm dbh and their phytosociological values for each quadrat group are shown in Tables 7.18 and 7.19. The species were ranked in terms of cover value index and total basal area. Seven species were among the 10 most important in both quadrat groups, with three of them, *Alseis longifolia*, *Maximiliana maripa* and *Simarouba amara*, showing similar values of relative density and dominance in both quadrat groups. This and the family and species composition indicate that the groups are floristically similar.

The number of seedlings of *Peltogyne* and *Pradosia* was higher in group 1, while for *Ecclinusa* the number of seedlings was similar between groups. These species had a similar mortality rate between quadrat groups and after 29 months only *Peltogyne* seedlings showed a statistical difference in growth rate between groups, with its seedlings growing faster in group 2 (Table 7.20). It is important to highlight that *L. kunthiana* had only two seedlings (quadrat group 2) in October 1991 and only one in March 1994. *Lecythis* did not have any seedlings in the quadrat groups.

In March 1994, a total of 533 *Peltogyne* seedling recruits were tagged in group 1, with a mean of 16 seedlings per quadrat. Sixty-one *Peltogyne* seedling recruits were tagged in group 2 (mean= 4 seedlings/quadrat). The mean numbers of seedling recruits per quadrat between the two groups were statistically different (t test, t= 4.51, p= 0.0001, df= 39).

The number of saplings per quadrat for *Ecclinusa*, *Peltogyne* and *Pradosia* are shown in Table 7.21. Only

Table 7.18. Species of trees ≥ 10 cm dbh occurring in the group 1 (0.66 ha) on Maracá Island, RR, Brazil with number of individuals, total basal area (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI). Species ranked by CVI and total basal area.

Group 1					
Species	Ni	BA (m^2)	RD (%)	RDo (%)	CVI (%)
Peltogyne gracilipes	75	10.54	23.73	49.38	73.11
Pradosia surinamensis	37	2.76	11.71	12.95	24.66
Maximiliana maripa	36	2.08	11.39	9.77	21.17
Lecythis corrugata	28	0.75	8.86	3.54	12.40
Ecclinusa guianensis	23	0.60	7.28	2.82	10.10
Simarouba amara	9	0.92	2.85	4.32	7.17
Tabebuia uleana	12	0.57	3.80	2.68	6.48
Alseis longifolia	15	0.20	4.75	0.92	5.67
Peltogyne paniculata	9	0.39	2.85	1.82	4.66
Vitex schomburgkiana	4	0.37	1.27	1.76	3.02
Picramnia cf. spruceana	7	0.13	2.22	0.61	2.82
Chomelia barbellata	6	0.17	1.90	0.78	2.68
Pouteria surumuensis	4	0.21	1.27	1.00	2.26
Himatanthus articulatus	5	0.08	1.58	0.36	1.94
Drypetes variabilis	2	0.21	0.63	0.98	1.62
Enterolobium schomburgkii	3	0.12	0.95	0.55	1.50
Eugenia cupulata	3	0.07	0.95	0.32	1.27
Genipa americana	2	0.12	0.63	0.55	1.18
Maytenus guianensis	3	0.04	0.95	0.17	1.12
Mauritia flexuosa	2	0.09	0.63	0.41	1.04
MTN 2791	1	0.14	0.32	0.68	1.00
Couepia paraensis	2	0.04	0.63	0.19	0.83
Spondias mombin	1	0.10	0.32	0.49	0.81
Guapira sp.	2	0.03	0.63	0.16	0.79
Cochlospermum orinocense	1	0.10	0.32	0.47	0.78
Machaerium sp.	2	0.02	0.63	0.11	0.74
Quiina cf. rhytidopus	2	0.02	0.63	0.09	0.72
Amaioua corymbosa	2	0.02	0.63	0.08	0.72
Licania apetala	1	0.07	0.32	0.33	0.65
Gustavia augusta	1	0.06	0.32	0.26	0.58
Hymenaea courbaril	1	0.05	0.32	0.25	0.57
Inga sp.	1	0.04	0.32	0.17	0.48
Eugenia sp.	1	0.03	0.32	0.14	0.46
Bauhinia ungulata	1	0.03	0.32	0.13	0.44
Xanthoxylum aff. rigidum	1	0.02	0.32	0.11	0.43
Tetragastris panamensis	1	0.02	0.32	0.11	0.43
Apeiba schomburgkii	1	0.02	0.32	0.10	0.42
Ryania speciosa	1	0.01	0.32	0.07	0.38
Cecropia sp.	1	0.01	0.32	0.06	0.37
Crepidospermum goudotianum	1	0.01	0.32	0.05	0.36
Lonchocarpus sp.	1	0.01	0.32	0.05	0.36
Swartzia laurifolia	1	0.01	0.32	0.05	0.36
Faramea crassiloba	1	0.01	0.32	0.04	0.36
Duroia eriopila	1	0.01	0.32	0.04	0.36
Machaerium biovulatum	1	0.01	0.32	0.04	0.35
Brosimum guianensis	1	0.01	0.32	0.04	0.35

Table 7.19. Species of trees ≥ 10 cm dbh occurring in the group 2 (0.42 ha) on Maracá Island, RR, Brazil with number of individuals, total basal area (BA), relative density (%), relative dominance(%) and cover value index. Species ranked in terms of CVI and total basal area.

Group 2					
Species	Ni	BA (m^2)	RD (%)	RDo (%)	CVI (%)
Lecythis corrugata	29	1.60	14.87	13.46	28.33
Peltogyne gracilipes	14	2.07	7.18	17.34	24.52
Ecclinusa guianensis	23	1.44	11.79	12.05	23.85
Pradosia surinamensis	10	1.79	5.13	14.99	20.12
Maximiliana maripa	13	0.83	6.67	6.96	13.63
Tetragastris panamensis	11	0.47	5.64	3.91	9.55
Simarouba amara	4	0.70	2.05	5.86	7.91
Duroia eriopila	10	0.20	5.13	1.70	6.83
Alseis longifolia	10	0.14	5.13	1.14	6.27
Couratari multiflora	2	0.44	1.03	3.71	4.74
Crepidospermum goudotianum	7	0.09	3.59	0.77	4.36
Himatanthus articulatus	6	0.14	3.08	1.16	4.23
Couepia paraensis	4	0.22	2.05	1.83	3.88
Eschweilera pedicellata	3	0.22	1.54	1.88	3.42
Protium crenatum	2	0.27	1.03	2.25	3.28
Pouteria surumuensis	4	0.09	2.05	0.79	2.84
Guatteria schomburgkiana	4	0.08	2.05	0.66	2.71
Licania kunthiana	2	0.19	1.03	1.58	2.61
Inga sp.1	3	0.11	1.54	0.90	2.44
Pouteria hispida	3	0.06	1.54	0.49	2.02
Mauritia flexuosa	2	0.10	1.03	0.85	1.88
Lonchocarpus sp.	3	0.04	1.54	0.33	1.87
Pouteria reticulata	2	0.10	1.03	0.83	1.85
Lueheopis duckeana	3	0.03	1.54	0.27	1.81
Brosimum guianensis	2	0.08	1.03	0.68	1.71
Agonandra silvatica	1	0.11	0.51	0.91	1.43
Amaioua corymbosa	2	0.03	1.03	0.22	1.25
Drypetes variabilis	2	0.02	1.03	0.21	1.23
MTN 2847	1	0.05	0.51	0.45	0.96
Licania minutiflora	1	0.03	0.51	0.26	0.78
Aniba hostmanniana	1	0.02	0.51	0.19	0.70
Oenocarpus bacaba	1	0.02	0.51	0.18	0.69
MTN 2864	1	0.02	0.51	0.18	0.69
Ficus sp.	1	0.02	0.51	0.18	0.69
Gustavia augusta	1	0.02	0.51	0.17	0.69
Picramnia cf. spruceana	1	0.01	0.51	0.12	0.63
Inga alba	1	0.01	0.51	0.12	0.63
MTN 2876	1	0.01	0.51	0.10	0.61
Cheiloclinum cognatum	1	0.01	0.51	0.08	0.59
Tabebuia uleana	1	0.01	0.51	0.08	0.59
Vitex schomburgkiana	1	0.01	0 51	0.07	0.59
Inga bourgonii	1	0.01	0.51	0.07	0.59

Table 7.20. Number of individuals, mean height, median height growth, and the percentage of mortality of seedlings of three tree species in the two transect quadrat groups on Maracá Island, Roraima, Brazil.

Species	N_0	Mean Height$_0$ (cm)	N_1	Median growth* (cm)	Mean Height$_1$ (cm)	% mort.
Ecclinusa						
Group 1	6	22.5	3	0.9	28.6	50.9
Group 2	9	20.6	5	1.5	31.5	44.4
Peltogyne						
Group 1	308	14.2	219	2.6	17.7	29.8
Group 2	94	16.2	66	3.3	19.6	29.8
p		0.03		0.02	n.s.	n.s.
Pradosia						
Group 1	36	15.3	13	1.5	17.4	63.9
Group 2	11	12.6	5	1.0	13.5	54.5
p		0.04		n.s.	n.s.	n.s.

$_0$ at the first measurement (October 1991).
$_1$ at the last measurement (March 1994).
* For survivors of the 29-month period (October 1991-March 1994).
p, Probabilities are for t-test (mean height), Mann-Whitney test (median growth) and Chi-square test (mortality). n.s.= not significant at $p > 0.05$.

Table 7.21. Total number of saplings (Nt), mean number per quadrat (16 m^2) of the three most important species tagged in October 1991 in the two quadrat groups on Maracá Island, Roraima, Brazil. Within columns same letters are not significantly diffrent ($p \geq 0.05$, one-way Anova, with Tukey test for multiple comparisons).

	Group 1			Group 2			
	Nt	Mean	sd	Nt	Mean	sd	P
Ecclinusa	8	0.6^a	±1.0	29	2.2^a	±4.9	n.s
Peltogyne	217	15.5^b	±7.8	83	6.4^a	±7.6	0.005
Pradosia	131	9.4^c	±7.9	36	2.8^a	±4.7	0.01

P, Probabilities are for t-test. n.s.= not significant at $p > 0.05$.

Ecclinusa did not have significant difference in the number of saplings per quadrat between quadrat groups. Within-quadrat group analyses showed that *Peltogyne* had more saplings than the other two species in quadrat group 1, but the numbers of saplings per quadrat among species were similar in quadrat group 2. *Licania* occurred with two saplings in group 1 and seven in group 2, while *Lecythis* had no saplings in group 1 and only one in group 2. Unlike the seedlings, the saplings were not remeasured after 29 months owing to logistic problems, so no data are available for their mortality and growth rates. However, the data from PRF and PPF plots showed that there is no difference in the growth rate of saplings between these forest types (see Chapter 6 for details).

DISCUSSION

Although the DCA and DCCA analyses showed that there is a gradient along the transects with quadrats from lower slope and plateau usually at opposite extremes of axis I, the environmental variables supplied in this study did not explain the floristic variation among quadrats. This finding suggests that other environmental variables such as topography and drainage could be the factors that are affecting the spatial distribution of the species. Topography has been regarded as the most important abiotic factor causing spatial variation in the structure of tropical forests on a local scale (Bourgeron 1983, Basnet 1992, Oliveira-Filho *et al.* 1994b), since it is often correlated with other important environmental variables such as ground water regime and the physical and chemical properties of the soils (Bourgeron 1983). Although topography could be an important factor in explaining the floristic gradient near the PRF in this particular case, it does not seem to be applicable in the wider context of this

forest type. On Maracá Island PRF also occurs in flat areas, in general near a river bank. Therefore, instead of topography, drainage seems to be the factor promoting this gradient. Several papers (e.g. Newbery *et al.* 1986, Furley & Ratter 1990, Oliveira-Filho *et al.* 1994a) have shown the importance of drainage in the distribution of plant communities. The soil pit descriptions (Appendix 1) showed that the first quadrat (lower slope) in transect 1 had poor drainage and a high water table level during the wet season. *Peltogyne* forest is subject to a high level of ground water during the peak of the wet season (D. Villela personal communication), although as already discussed in Chapters 4 and 5, this forest type is not related to flooded areas and occurs often in well-drained soils.

Johnston (1992) found that topography seemed to control differences in soil moisture in a *Tabonuco* forest in Puerto Rico, with Ca and Mg appearing to move freely between upper and lower slope positions. The concentration of nutrients in the surface soils did not vary along the transects, suggesting that the drainage or the surface runoff is not important in the dynamics of those elements and so high losses of nutrients by leaching probably do not occur. Thus, the drainage effects, if they exist, seem to be related to a drought, that might occur mainly in the plateau quadrats, rather than an indirect effect on soil properties. The strong correlation found beteween Mg concentrations and the number of *Peltogyne* trees, is an evidence that *Peltogyne* abundance rather than drainage is affecting the Mg concentration on the surface. Therefore, *Peltogyne* Mg-rich litter coupled to parent material, as discussed in Chapter 4, seem to be the factors related to Mg concentrations on PRF soils, with parent material being more related to the highest concentrations of Mg in the deepest horizon.

Ecclinusa, *Lecythis* and *Tetragastris panamensis* (abundant in group 2 from TWINSPAN analyses) have been characterised as a common species on Maracá forests (Milliken & Ratter 1989), occurring among the most important

species in both PRF and FWP. However, the results suggest that there is competition between these species and *Peltogyne*, since they occurred in group 1 with many fewer individuals most of which were in the smallest dbh classes.

Although the majority of individuals of *Peltogyne* (seedlings, saplings and trees) were in group 1, the occurrence of seedlings and saplings of this species in group 2, with similar rates of mortality and growth as in group 1, together with the fact that *Peltogyne* trees also showed a good tree recruitment in group 2 suggest that the PRF is extending across its boundary with PPF.

CONCLUSION

The floristic and regeneration data indicate that *Peltogyne* has a stable, regenerating populations along the transects with a clear preference for the middle-slope and lower-slope quadrats. The species showed no differences in seedling mortality between lower and plateau quadrats and a faster growth in the latter. These data suggest that the PRF is expanding.

The DCCA analyses showed that the soil variables investigated did not explain the floristic gradient of the transects, although *Peltogyne* density was strongly correlated with Mg concentrations. Other factors such as drainage might be promoting this gradient and so the *Peltogyne* dominance in the middle-lower slope quadrats, but it is noteworthy that elsewhere its density is not related to drainage.

Chapter 8. Post-dispersal seed predation on *Peltogyne*.

INTRODUCTION

It is often assumed but not frequently demonstrated that seed predators can reduce seedling recruitment (Andersen 1987; Sork 1987; Louda 1989; and Schupp 1990). Much research on invertebrate seed-predators has concerned host-specific beetles on leguminous trees (Janzen 1969, 1970, 1971, 1980). The few investigations of seed-predation by ants have been made mainly in Australian woodland and desert vegetation (Mares & Rosenzweig 1978, Davidson 1977, Abramsky 1983, Andersen & Ashton 1985). In this chapter I report an instance of seed predation by beetles and leaf-cutter ants in the *Peltogyne* study plots.

Peltogyne did not flower in 1991, 1993 and 1994. However, it had a substantial wet-season flowering from May to August 1992 and its fruits were matured by December 1992. Its fruits are dehiscent, woody, 25-31 mm long and 15-19 mm wide, with one hard and flat seed (13-17 mm long, mean air-dry weight 0.27-0.47 g) which is wind dispersed. By February 1993 all study plots in PRF and PPF had a large number of *Peltogyne* seeds on the ground.

MATERIALS AND METHODS

ANT PREDATION

In late February 1993 many *Peltogyne* seeds were found being carried by ants and deposited on their trails. Most of the seeds were hard and undamaged. Seed bait experiments, using intact seeds collected in the PRF plots, were made near a nest of *Atta cephalotes* L. (on 6 March 1993) and another of a *Trachymyrmex* sp (on 8 March 1993) which were

about 600 m from each other and both in PPF. The *Atta* were nocturnal while the *Trachymyrmex* were active night and day. *Peltogyne* seeds were placed in groups about 3 m apart on each of the ant trails. On the *Atta* trail there were four groups, each with twenty-five hard unmoistened seeds and twenty-five soft imbibed seeds, and on the *Trachymyrmex* trail seven groups each with ten seeds in each category . All seeds were numbered by water-proof black ink and checked after 24 h (*Atta*) or 8 h (*Trachymyrmex*).

PREDATION BY OTHER ORGANISMS

Post-dispersal seed predation of *P. gracilipes* was measured twice in March 1993, when only 19% of the adult trees (out of 91 individuals) still had some attached fruits. Three 50 cm x 50 cm quadrats were placed in a stratified random manner in each of three 50 m x 50 m plots in PPF and three similar plots in PRF on 6 March 1993. In the first census all *Peltogyne* seeds in each quadrat were collected and separated into two categories: not damaged; and damaged or aborted. The damage was caused by beetles and possibly other invertebrates. Many of the seeds showed evidence of fungal attack but it is not known if this was a primary cause of damage. A second sampling was made in a similar manner in newly located quadrats on 20 March, when some seeds had already germinated.

RESULTS AND DISCUSSION

The seeds within the quadrats from the PRF were always more attacked (both censuses; Table 8.1). The rates of predation (4.5-20.9%) can be considered low, given that specialist and generalist beetles frequently destroy 90-100% of a seed crop (Janzen 1969, 1971). Two species of beetles from two families, Curculionidae and Nitidulidae, were collected from *Peltogyne* seeds. The latter family includes

Table 8.1. Average numbers (± S.D.) of all *Peltogyne gracilipes* seeds, the percentage of seeds which were beetle damaged, and the percentage of seeds which were damaged from any cause in three 50 cm x 50 cm quadrats in three plots in each of PPF and PRF on Maracá Island, Brazil. Data are given for (a) 6 March 1993 and (b) 20 March 1993.

Plot		Number of seeds (m^{-2})	Beetle-damaged seeds (%)	Damaged seeds (all causes) (%)
PPF				
7	a	79 ± 63	1.7	6.3
	b	56 ± 56	2.4	19.6
8	a	85 ± 94	0	0
	b	133 ±182	7.0	11.3
9	a	0	-	-
	b	0	-	-
PRFa				
1	a	441 ± 206	4.5	9.1
	b	376 ± 162	9.6	14.6
2	a	120 ± 29	8.9	14.2
	b	153 ± 154	20.9	22.9
3	a	80 ± 52	5.0	8.7
	b	124 ± 49	16.1	18.5

many well-known pests of wood.

Although beetle attack was low, much damage was caused by leaf-cutting ants in one of the PPF plots. This plot had been observed to have a high seed density on 6 February 1993. Two weeks later the ants (*Atta cephalotes* L.) had removed all *Peltogyne* seeds from the entire plot (Table 8.1) and a large number of intact seeds was found temporarily stored on ant trails near it (Fig. 8.1).

On both bait trails all the imbibed seeds, and 34% (*Atta*) and 26% (*Trachymyrmex*) of the hard seeds were removed. Some of the hard seeds were removed only a short distance (often < 50 cm) from where they were originally placed and these results confirmed the field observations that only imbibed seeds were transported to the nests. By 15 April 1993, after several rainy days, all the *Peltogyne* seeds on ant trails had been removed. Soldiers carried large pieces of seeds or sometimes a whole seed, while workers carried only small pieces (Fig. 8.2). Although I have no quantitative data, most of seeds that were observed being transported by ants had been cut up.

The ants seemed to have an important influence in the plot from which the seed removal was observed since there were no *Peltogyne* seedlings in five 2 m x 1 m sub-plots sampled from 15 October 1991 to 16 March 1994. Similar samples in the other plots showed recruitment (from October 1991 to March 1994) with the highest values always in PRF (Table 8.2). All recruits resulted from the high seed production in December 1992-March 1993 and no seeds were produced in the corresponding period of 1993-1994. The first measurement was made on 22 March 1993 at the end of the dry season. The second measurement on 15 March 1994 includes those seeds which germinated during the wet season of 1993.

Some papers have shown that ants play an important role in seed dispersal in some communities, mainly in Australia and South Africa (e.g. Hughes *et al.* 1993). However little is known about this phenomenon in neotropical rain forests. According to Galetti & Rodrigues (1992), ants play a

Figure 8.1. *Peltogyne* seeds on ant trail in PPF on Maracá Island, Brazil.

Figure 8.2. Leaf-cutting ants attacking *Peltogyne* seeds in PPF on Maracá Island, Brazil.

Table 8.2. Mean number (± S.D.) of *Peltogyne* seedlings (on 15 October 1991) and the new recruits: (a) on 22 March 1993; and (b) on 15 March 1994 in each plot in PPF and PRF on Maracá Island, Brazil.

Plot	No. of seedlings (m^{-2})	No. of recruits (m^{-2})	
		(a)	(b)
PPF			
7	0.1±0.2	0.4±0.4	1.5±1.3
8	5.7±4.5	1.8±2.5	4.8±6.5
9	0	0	0
PRFa			
1	6.1±4.5	3.5±3.2	24.5±24.1
2	8.1±3.2	2.6±1.5	9.1±6.1
3	23.3±29.9	2.0±3.7	7.7±5.9

secondary role in the seed dispersal of *Inga* sp. in a Brazilian semi-deciduous forest. The observation that leaf-cutter ants cut up most of the *Peltogyne* seeds before removing them to their nests suggests that dispersal is negligible or much subordinate to predation. *Peltogyne* seeds do not bear any substance attractive to ants such as arils or oil-rich appendages which are common in some Australian myrmecochophorous plants (Hughes *et al.* 1993). Roberts & Heithaus (1986) studying the secondary movements of the very small seeds of *Ficus hondurensis* in a dry forest in Costa Rica found that ants (*Atta cephalotes* was the most conspicuous) removed up to 97.7% of them, although some fig seeds may survive and benefit from ant dispersal. Levey & Byrne (1993) found that leaf-litter ants (*Pheidole* spp.) both eat and disperse *Miconia* seeds in Costa Rica. In degraded areas in Amazônia two ant species *Pheidole puttemansi* and *Solenopsis aurea* prey on seeds weighing less than 0.2 g while a leaf-cutter ant species (*Atta sexdens*) has been reported to attack both medium-sized seeds (0.1 to 1.0 g) and tree seedlings (Moutinho *et al.* 1993). The *Peltogyne* seeds fall into the medium-size category (mean 0.38 g).

Although the density of mature *Atta cephalotes* colonies in Maracá forest is very low (0.051 ha^{-1}), they are clumped (Jaffe & Vilela 1989) and so might have a considerable local effect on the plant population. Leaf-cutting ants were also observed attacking *Peltogyne* seeds in the PRF 4 plot in a similar way to that observed in PPF.

CONCLUSION

It is not known how far ants might be responsible for the local distribution of *Peltogyne* on Maracá or for tropical trees in general. The rôle of ants in seed dispersal and predation in neotropical forests should be further investigated.

Chapter 9. Herbivory on seedlings and trees of three non-pioneer species in three forest types on Maracá Island, Brazil.

INTRODUCTION

It is well known that herbivory can affect the survival, growth and reproduction of plants (Marquis 1984, Crawley 1985, Clark & Clark 1985, Gauge & Brown 1989, Nascimento & Hay 1994), thereby affecting a plant's competitive ability, in both evolutionary and ecological time scales (Coley *et al.* 1985). The rate of foliar herbivory may be affected by factors such as leaf age, leaf quality, plant size, (Coley 1983a, Marquis 1987, Ernest 1989, Aide 1992, Kursar & Coley 1992, Nascimento & Hay 1993) and by the composition, density and diversity of the surrounding vegetation (Brown & Ewel 1987). The number of insects per plant and per unit area and their damage to leaves are usually held to be higher in monospecific stands than in species-rich ecosystems (eg. Crawley 1983). Brown & Ewel (1987) pointed out that although studies on herbivory have been made on numerous ecosystems, simultaneous comparisons of herbivory rates in species-rich and species-poor ecosystems in the same environment are lacking.

The major aim of this study was to test the hypotheses that the *Peltogyne*-rich forest, as a monodominant stand, is particularly prone to herbivore damage, but that the *Peltogyne* seedlings do not suffer mortality by density dependent herbivory (Janzen-Connell model). Two components of intraspecific variation in leaf herbivory were measured: 1) the variation between individuals in the population at any one time and 2) the temporal variation in rates of damage to each individual.

METHODS

STUDY SPECIES

Three non-pioneer species, according to Swaine & Whitmore's (1988) classification, were chosen for this study because of their abundance in all size classes and their ease of identification in the field. One of them is the *Peltogyne* in PRF, the others are an understorey species (*Ecclinusa guianensis*) and a canopy species (*Pradosia surinamensis*) both common in Maracá forests. *Peltogyne* is deciduous as trees and has bifoliate leaves, with each leaflet entire, oblong-lanceolate in shape and coriaceous (Silva 1976, Lewis & Owen 1989). In this study each leaflet was considered as a leaf. *Ecclinusa guianensis* and *Pradosia surinamensis* (henceforth in this Chapter referred to by their generic names only) are evergreen tree species, with simple leaves which contain latex. For details about density and basal area of these species in Maracá forests see chapter 4.

STUDY SITES

The study was carried out in the same plots of PRFa, PPF, and FWPa used for floristic descriptions (see Chapter 3) and in a medium gap (33 m long and 11 m wide) (Brokaw 1985) near one of the plots of the PRFa.

DISCRETE SAMPLING METHOD

In November 1991, all leaves of *Ecclinusa*, *Peltogyne* and *Pradosia* in the litterfall collected from 11 traps (each 0.33 m^2) in each of the three plots in each forest type had their outline traced on graph paper. The leaves were

individually examined and leaf area removed was visually estimated using a ten-point scale: 0, < 10%, 10-20%, 20-30%, 30-40%, 40-50%, 50-60%, 60-70%, 70-80%, 80-90%, and 90-100%. The damage was assumed to have been caused by chewing insects before the leaves fell into the traps. Mean leaf herbivory for each plot was calculated by multiplying the number of leaves within each damage class by the mean of that class to provide a percentage apparent leaf damage estimate (Wint 1983).

On 8-9 June 1992, at each of the three plots in each forest type, five seedlings (≤ 50 cm tall) of each study species were chosen randomly. All leaves from each individual were removed and their herbivore damage assessed as above after the leaves had been separated into two age categories: young and mature (Young leaves were not fully expanded, their colour was light-green and they were nearest to the tips of the branches. Mature leaves were fully expanded, dark green and they were located, in general, below the tip).

Leaf herbivory values were transformed (ln (% damaged leaf area +1), Coley 1983a) to obtain a normal distribution, and comparisons among species within forest types and among forests within species were made by two-way Nested Anova where factor A (forest type) was considered fixed and factor B (plot) random (Zar 1984). Differences among means were calculated using Tukey's test. A Chi-square test was applied for comparisons of the proportion of damaged leaves between young and mature leaves.

TEMPORAL VARIATION

This part of the study was only carried out for *Peltogyne* in PRF, for *Pradosia* in FWP, and for both these species in a gap located near to one of the plots of PRF.

On 1-5 August 1991 ten seedlings (≤ 50 cm tall) of each species (*Peltogyne* and *Pradosia*) were chosen at random in

each study site. At least three leaves, independent of leaf age category, on each plant were traced and left intact on the plant. As for the discrete method, leaves were classified into two age categories: young and mature. Young leaves (group 1) were about 14 d old, while most of mature leaves (group 2) had probably been produced in the past wet season and so were about 1 yr old. After one month (1-5 September 1991) the plants were censused for changes in the damaged area on each traced leaf, and for leaf fall and leaf production. The young leaves which were not fully expanded when marked were redrawn in the second census to allow for their increased area. Further censuses were made every two months until July 1992. Leaf area was measured using a planimeter. The area of insect damage was determined by counting the number of squares (mm^{-2}) visible under the damaged area.

EARLY HERBIVORY IN *PELTOGYNE* SEEDLING RECRUITS

The foliar herbivory on the *Peltogyne* seedling recruits tagged in March 1993 (see Chapter 6) was visually estimated using the scoring classes, as already explained in the previous section. The plants were about 13 d old and still had both cotyledons. Most leaves were not fully expanded.

HERBIVORES

At each sampling date, all plants sampled were checked for the presence of herbivores or for evidence of mammalian attack. All insects (larvae and adults) that were observed feeding on leaves of the tagged plants were collected.

RESULTS

DISCRETE METHOD

Leaf litterfall

Percentage "apparent" leaf damage from the litterfall sampling for *Ecclinusa, Peltogyne,* and *Pradosia* are shown in Table 9.1. There were no differences within species between forests (t-tests, $p > 0.17$). However, there was a significant difference among species (one-way Anova, $F= 12.6$, $p= 0.001$). This difference reflected the markedly lower herbivory in *Pradosia*.

Seedling leaves

As for leaf litterfall (above), there were no differences in leaf herbivory for seedlings within species between forests nor among species within forest types (Table 9.2). The high coefficients of variation for seedlings of all study species were caused by a small number of heavily damaged individuals while the average extent of damage was low (Fig. 9.1). The number of damaged leaves was, in general, higher in mature leaves, except for *Peltogyne* which had a similar proportion of damage among leaf age categories (Table 9.3). In the majority of individuals of all species, mature leaves had more damage than young leaves (Table 9.3).

TEMPORAL VARIATION

The median herbivory rates on leaves from group 1 and group 2 (Table 9.4) of *Peltogyne* and *Pradosia* were not

Table 9.1. The percentage leaf area removed by herbivores from leaves (collected as litterfall) in three species in each of three plots in three forest types on Maracá Island, Roraima, Brazil.

Forest	*Peltogyne*	*Pradosia*	*Ecclinusa*
PRFa			
Plot 1	7.7	6.2	-
Plot 2	11.5	5.3	-
Plot 3	15.1	9.7	12.6
Mean	**11.4**	**7.1**	
PPF			
Plot 7	19.5	-	-
Plot 8	17.0	-	-
Plot 9	13.4	-	-
Mean	**16.6**		
FWPa			
Plot 10	-	5.0	8.3
Plot 11	-	4.0	11.1
Plot 12	-	6.4	14.2
Mean		**5.1**	**11.2**

Table 9.2. Mean values (with ranges) of percentage leaf damage area from seedlings of three species in each study forest type on Maracá Island, Roraima, Brazil.

	PRFa	PPF	FWPa	p
Peltogyne				
Mean	2.3	3.8	-	n.s.
range	(0-9)	(0-7.7)		
CV	126	82		
Pradosia				
Mean	9.0	7.2	11.9	n.s.
range	(0-22.5)	(0-33.7)	(0-35)	
CV	83	127	95	
Ecclinusa				
Mean	9.0	11.9	9.5	n.s.
range	(0-24.3)	(1.2-53)	(0-38.6)	
CV	88	119	103	
p	n.s	n.s	n.s.	

CV= Coefficient of variation (%).
p= probabilities, n.s= not significant.

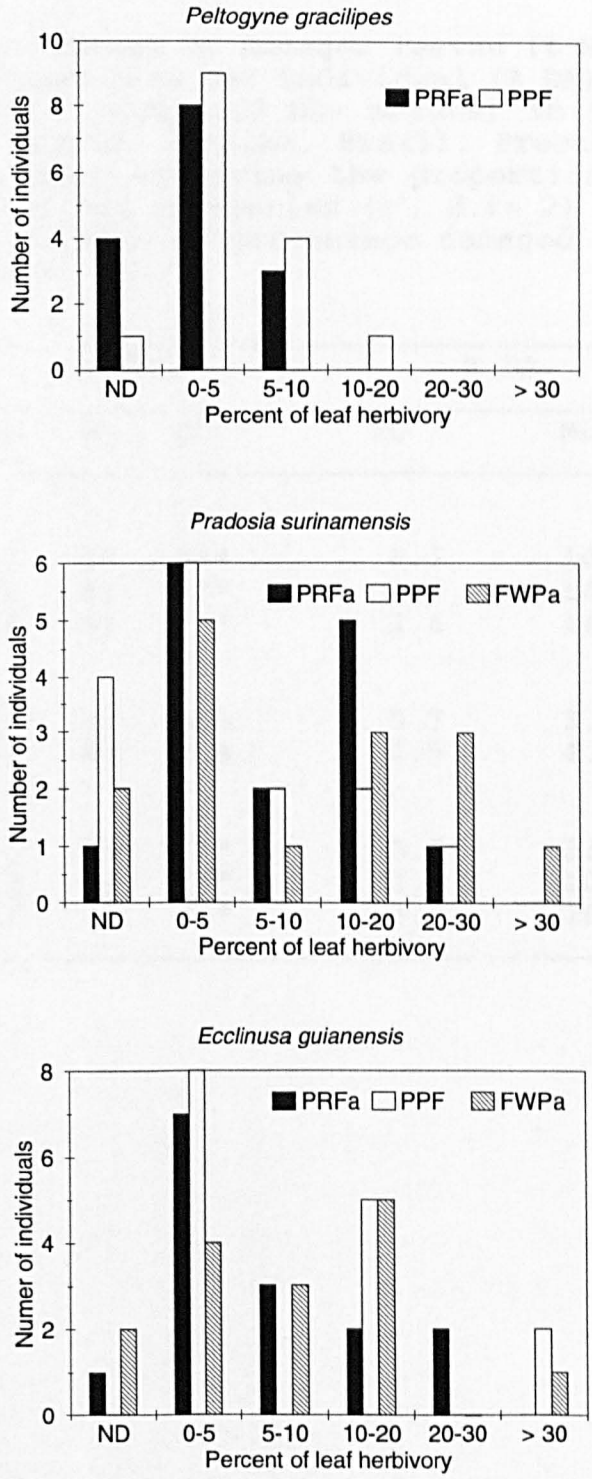

Figure 9.1- Intraspecific variation in leaf herbivory on seedlings (< 50 cm tall) of three study species in PRFa, PPF, and FWPa.

Table 9.3. The percentage of damaged leaves (% NDL) and mean of percentage damaged area per individual (% DA) in two leaf age categories (YL= young and ML= mature) in three forest types on Maracá Island, Roraima, Brazil. Probabilities are for a Chi-square test comparing the proportion of damaged leaves between leaf age categories ($p^{£}$, d.f= 2) and for a t-test comparing the means of percentage damaged area between leaf age categories ($p^{&}$).

	% NDL			% DA		
	YL	ML	$p^{£}$	YL	ML	$p^{&}$
Ecclinusa						
PRFa	17	57	***	6.3	10.3	**
PPF	16	53	***	0.5	14.2	***
FWPa	16	59	***	2.4	11.2	***
Peltogyne						
PRFa	12	30	n.s.	0.7	3.3	*
PPF	31	48	n.s.	1.5	4.5	**
Pradosia						
PRFa	5	60	***	3.7	13.8	***
PPF	18	54	***	3.0	10.2	n.s.
FWPa	33	73	***	3.0	16.3	***

significantly different within species and between species (Mann-Whitney test, $p > 0.05$). The proportions between species of damaged leaves over the 11-month period differed in the gap (Chi-square test= 4.54, d.f.= 1, $p \leq 0.05$), and this difference was a result of fewer leaves attacked in *Peltogyne*, but they were similar in the forest (Chi-square test= 1.45, d.f.= 1, $p \leq 0.05$). Within-species analysis showed that for *Peltogyne* the number of leaves attacked by herbivores was not different between the gap and forest (Chi-square= 1.92, d.f.= 1, $p > 0.05$), but for *Pradosia* it was (Chi-square test= 4.64, d.f.= 1, $p \leq 0.05$). Coefficients of variation ranged from 1.74 to 3.23 (Table 9.4) indicating that the variation in herbivory between plants is high in both species with herbivory rates positively skewed so that the modal individuals suffered less damage than the mean. All leaf damage to both species in the forest occurred during the wet season. However, in the gap only 50% (*Peltogyne*) and 35% (*Pradosia*) of the leaf damage occurred in the wet season. The damage on particular individuals were not constant over time for both species. For each sample period a different group of individuals was more heavily attacked.

The leaf fall over the 11-month period in the gap (41%, *Peltogyne* and 44%, *Pradosia*) was lower than that found for the forest (63%, for both *Peltogyne* and *Pradosia*) (Chi-square tests, $p \leq 0.01$). There were no significant differences in leaf fall between species in both site types (Chi-square tests, $p > 0.05$), with both species shedding more leaves during the dry season (Table 9.4).

The leaf production per individual over the 11-month period was similar between species in both site types. However, they differed in relation to the seasonal pattern (Table 9.4). For *Peltogyne*, 62% of the leaf production in the gap occurred in the dry season, while in the forest the percentage was only 25%. *Pradosia* produced a similar proportion of leaves in the dry (44% in the gap and 46% in the forest) and wet seasons (50% in the gap and 54% in the

Table 9.4. Herbivory rates (mean, coefficient of variation and median) per individual in each leaf age category, and percentage of leaf fall and leaf production per individual of *Peltogyne* and *Pradosia* over an 11-month period on Maracá Island, Roraima, Brazil.

	Group 1			Group 2			Dry season	
Species	Mean (%/day)	CV (%)	Median (%)	Mean (%/day)	CV (%)	Median (%)	Leaf fall (%)	Leaf prod. (%)
Peltogyne								
Gap	0.0044	252	0.00	0.0011	323	0.00	78	62
PRF	0.0005	300	0.00	0	0	0.00	81	25
Pradosia								
Gap	0.0352	255	1.94	0.0476	174	0.00	48	46
FWP	0.0205	204	0.00	0	0	0.00	70	44

forest) in both site types.

Herbivory rates were not correlated with plant survival, since the dead plants (two for *Peltogyne* and three for *Pradosia*) did not suffer any damage to their leaves during the study, with their aerial biomass in most cases totally dried.

HERBIVORY IN *PELTOGYNE* SEEDLING RECRUITS

The herbivory on leaves of new seedlings of *Peltogyne* was low in both PRF and PPF. After about 13 days of the germination only six of 81 (PRF) and two of 22 (PPF) newly tagged seedlings were attacked, with most seedlings (five from eight) with less than 5% of leaf area lost. At this time only 23% (PRF) and 27% (PPF) of the individuals had leaves fully expanded.

HERBIVORES

During the study, no herbivorous insects were collected from *Peltogyne* seedling leaves. For *Pradosia*, on only two occasions two different species of Lepidoptera caterpillars (one individual at the first time and three individuals of a different species, at the second time) were collected attacking its leaves. Unfortunately, they did not survive until adulthood in the laboratory and so they were not identified.

During the 11-month study no evidence of seedlings dying as a result of mammalian predation were found.

DISCUSSION

HERBIVORY IN THE LITTERFALL LEAVES

The mean herbivory values for the litterfall leaves in the three study species (range 5.1-16.6%) are within the range for defoliation levels of tropical rain forest (5-15%) suggested by Landsberg & Ohmart (1989), although Lowman (1984) highlighted that the levels of herbivory in most studies may have been underestimated since they have used the discrete sampling method.

Although the values of herbivory in this study may be underestimated, comparisons with other studies that used similar techniques are possible. The values of herbivory for *Ecclinusa, Peltogyne* and *Pradosia* were similar to an overall value of 11.3% (Scott 1990) for leaf-hole area in litterfall leaves of a range of species in FWPb (Thompson *et al.* 1992a) about 2-4 km distant from the PRFa. However they were, in general, higher than the mean values found for saplings (5%, Newbery & de Foresta 1985) and for canopy trees (5.3%-6.0%, Sterck *et al.* 1992) in rain forests in French Guiana.

DEFOLIATION ON *PELTOGYNE*

A remarkable herbivory event on *Peltogyne* was recorded in April 1992 when the trees were undergoing their annual leaf change (Nascimento & Proctor 1994, Appendix 3). The leaves were attacked by larvae of a wide-ranging moth species, *Eulepidotis phrygionia*. Only trees (≥ 10 cm dbh) with new leaves were attacked and not seedlings. This event was not repeated in 1993 and 1994. Therefore, although the herbivory levels of *Peltogyne* leaves from the litterfall samples (11.4%, PRF and 16.6%, PPF) are similar to the

values found by Scott (1990) for a community-wide sample in a FWP on Maracá, they seem to reflect a background level of mature leaf consumption which is unrelated to the infestation of new leaves.

Although occasional defoliation by herbivores can occur in *Peltogyne* trees which are flushing new leaves (Nascimento & Proctor 1994), the values of herbivory in this study do not support the suggestion that a species suffers less herbivory in species-rich ecosystems (Brown & Ewel 1987). However, further work is necessary since the observations of this study are based on 4-year data (1991-1994) and no data are available on the periodicity of caterpillar outbreaks in both PRF and FWP. Nascimento (1989) also found low levels of foliar herbivory (2.0-2.6%) using the discrete method on trees of *Vochysia divergens* a monodominant tree species in a flooded forest in Pantanal, central Brazil. It is important to highlight, however, that it is not known if *V. divergens* may suffer a massive attack like that observed for *Peltogyne* and with what frequency this kind of attack may occur in a monodominant stand.

FOLIAR HERBIVORY ON SEEDLINGS

Coley *et al.* (1985) proposed that the intrinsic growth rate of a species determines defences. This hypothesis predicts that slower growing species would be better defended and have lower herbivory rates than faster growing species. The species in this study are slow growing (see Chapter 6) and their herbivory rates, especially for *Peltogyne*, found by both discrete and long term methods, may be considered low when compared with other forest species (Lowman 1982; Coley 1983a,b; Lowman 1984; Marquis 1987; Nascimento & Hay 1993). However, as found in other studies (Coley 1983b; Nascimento & Hay 1993), variation in herbivory between plants at any one sample period was high, and rates

of damage to a particular individual were not constant with time.

Site is one of the factors that affects herbivory in plants (Brown & Ewel 1987; Marquis 1987). This was not observed for any of the study species, however, since no statistical differences between forest types were seen.

The differences found by the discrete method for the percentage of herbivory between young and mature leaves in all the study species is probably related to the fact that this method reveals damage that is accumulated during leaf development. The temporal variation method, however, showed that herbivory rates between leaves from group 1 (young leaves when plants were firstly mapped) and group 2 (mature leaves) were not different.

Many authors consider that the impact of leaf damage decreases with plant age or height or both (Marquis 1984; Nascimento & Hay 1994), so the smallest plants should have more defences. The low levels of herbivory found for the new seedlings of *Peltogyne* and established seedlings suggest that this species invests more in defence in the smallest size classes.

Herbivory in seedlings of *Peltogyne* seems not be density-dependent, since no statistical differences were found between PRF and PPF (see Chapter 6 for details of seedling density in PRF and PPF).

Molofsky & Fisher (1993) found that mammalian predation was an important component of mortality during the first year of seedling life for two (*Gustavia superba* and *Virola surinamensis*) of the three species studied by them in the seasonal moist forest of Barro Colorado, Panama. Although no exclosure experiment was made in PRF, during the 11-month study (from August 1991 to July 1992) and also during the first two weeks after the germination of some *Peltogyne* seeds (March 1993) no sign of mammalian predation was found in the study plots.

CONCLUSION

The leaf herbivory rates of trees and seedlings of the three study species were in the range for the tropical plants. The finds here seem to support the hypotheses that *Peltogyne* is prone to high levels of herbivory, since occasional massive defoliation can occur mainly when most trees are flushing new leaves simultaneously , but its seedlings do not suffer mortality due to density dependent herbivory (Janzen-Connell model).

Chapter 10. Are there allelopathic effects of *Peltogyne*?

INTRODUCTION

Allelopathy is a frequently postulated, but rarely proven, mechanism by which a species may exert influences on other species, by releasing chemical compounds into the environment and inhibiting the growth of surrounding organisms (Turner & Quaterman 1975). These chemical compounds can be produced in different organs of the plants depending on the species or even in different parts of the same plant (Rice 1974, Lawrence *et al.* 1991). Some studies on tropical plants (e.g. Válio 1973, Zaidan *et al.* 1985) have shown that the exudate of seeds of some species can have an effect on the germination of other species. Mabberley (1992) gave examples for tropical rain forests in which some species of *Croton* (Euphorbiaceae) and *Piper* (Piperaceae) produce chemicals that inhibit seed germination. He also suggested (without evidence) that the Brazil nut, *Bertholletia excelsa* (Lecythidaceae) may produce toxic litter. Therefore, allelopathy might be one of the mechanisms to explain the dominance of a single species, since it might reduce the productivity and vigour of individuals near the dominant species (Muller 1966, Gant & Clebsch 1975).

The aims of this study were to assess whether there is an allelopathic interference of *Peltogyne* on other plants and whether this mechanism could explain its dominance.

MATERIALS AND METHODS

Three experiments were made in the field laboratory of the Maracá Ecological Station to test allelopathy by *Peltogyne*. The first two experiments were designed to check whether the *Peltogyne* leaves have any effect on the germination of other species, while the third was designed to test if the *Peltogyne* seeds have any inhibitory effect on the germination of other species. Seeds of the other three species used in the experiments were: *Peltogyne paniculata*, *Phaseolus vulgaris* and *Tamarindus indica*. Only the first species is indigenous to Maracá where it is found occasionally in PRF, PPF and FWP. It was selected because the seeds were readily available and had a good germination rate. *P. vulgaris* and *T. indica* do not occur on Maracá and might be expected to be more vulnerable than *P. paniculata* to any allelopathic compound produced by *Peltogyne*.

EXPERIMENT 1

Five seeds of *T. indica* and *P. paniculata* (both Caesalpiniaceae), were used in each of three treatments: A (control), B and C. The seeds of *T. indica* were gathered on 14 April 1992 in an orchard located in the 'Maloca do Boqueirão' about 30 km south from Maracá Island. *P. paniculata* seeds were collected in early April 1992 in the forest near 'Casa de Santa Rosa' about 3 km from the field station. The soil used in all treatments was collected in FWP near the field station and it was similar to that described for FWPb (chapter 4). In each treatment, five seeds of each species were planted in black plastic bags (30 cm x 15 cm), one seed per bag. In treatment B, a litter layer composed of 10 g of *Peltogyne* litter was put on the soil of each bag. The litter sample (fresh litter) was gathered from beneath *Peltogyne* trees on 11 March 1992 (end of dry season), placed in an uncovered plastic tray and

stored in the laboratory until the beginning of the experiment (17 April 1992). The seeds from control and treatment B were watered with deionized water, while in treatment C the seeds were watered with a plant extract. The extract was made by grinding 10 g of air-dried fresh leaves, soaking in 100 ml of deionized water, for 12 h, and filtering through Whatman No. 1 filter papers. The experiment lasted for 25 d. After that period all plants were measured for shoot height and dry weight.

EXPERIMENT 2

Starting on 19 June 1992 and finishing on 17 July 1992 for *T. indica* and *P. paniculata* seeds and starting on 24 June 1992 and finishing on 2 August 1992 for *P. vulgaris*, this experiment had three different treatments: D (control), E, and F. In each treatment a total of ten seeds per species (*T. indica, P. paniculata* and *P. vulgaris*) were used. Two seeds of each species were planted in the plastic bags described above and each bag had only seeds from the same species. In treatment D the seeds were planted in soil from FWP and watered with deionized water. In treatment E the seeds were planted in soils from PRF and watered with deionized water. Seeds for treatment F were planted in soils from FWP, as in the control, but watered with *Peltogyne* leaf extract. The extract was made in the similar way to that described for experiment 1. At the end of the experiment the plants were measured for shoot height and root length.

EXPERIMENT 3

Thirty *Peltogyne* seeds were planted on 11 March 1993, one per plastic bag. The *Peltogyne* seeds used in this experiment were gathered in PRFa on 25 February 1993. After 8 d, when most *Peltogyne* seeds were germinating, one seed of

Phaseolus vulgaris (n=15) was planted in 15 randomly chosen bags that had one *Peltogyne* seed germinating (treatment H). The *Phaseolus vulgaris* seed, in each bag, was planted about 1 cm from the *Peltogyne* seed. Other *P. vulgaris* seeds (n=15) were planted in separate bags and used as controls (treatment G). In all treatments, the soils were watered with deionized water. The experiment was finished on 23 March 1993, with all plants being measured for shoot and root length.

Statistical analysis

In each experiment, a one-way ANOVA was carried out to compare the mean shoot and root growth rates (only in experiment 3) among treatments for each species, with the significance level set to 0.05 (Zar 1984). A Dunnett test was used for multiple comparisons when a significant result was obtained by the ANOVA.

RESULTS

A summary of the results for each experiment is given in Tables 10.1 and 10.2. All the study species, except *P. paniculata* in experiment 1, did not show any statistical difference between control mean and treatment means for both shoot height and root length. The result for experiment 1 indicated that *P. paniculata* grew significantly better in soils covered by *Peltogyne* leaf litter or watered with *Peltogyne* leaf extract. The germination rates of the species were also similar between control and the other treatments in all experiments, with the rates in most cases higher than 60%.

Table 10.1. Mean shoot height (SH) and dry weight (DW) of *Tamarindus indica* and *Peltogyne paniculata* at the end of experiment 1 in which seedlings of these species were subjected to three allelopathy treatments as described in the text. p values are for one-way Anova.

	SH (cm)		DW (g)		SH (cm)		DW (g)	
	Mean	sd	Mean	sd	Mean	sd	Mean	sd
	Tamarindus indica				*Peltogyne paniculata*			
Treatment								
Control	7.0	7.8	0.20	0.20	4.2	5.8	0.06	0.08
B	10.4	6.9	0.25	0.14	11.5	0.7	0.15	0.02
C	1.6	3.6	0.13	0.18	10.7	0.9	0.19	0.03
p	0.13		0.58		0.01		0.01	

Table 10.2. Mean shoot height (SH) and root length (RL) of *Phaseolus vulgaris* and *Peltogyne paniculata* at the end of experiments 2 and 3 in which seedlings of these species were subjected to three allelopathy treatments as described in the text. p values are for one-way Anova or t-test.

	SH (cm)		RL (cm)		SH (cm)		RL (cm)	
	Mean	sd	Mean	sd	Mean	sd	Mean	sd
Experiment 2	*Phaseolus vulgaris*				*Peltogyne paniculata*			
Treatment								
Control	12.6	9.5	8.1	5.3	9.6	4.0	8.8	3.9
E	15.4	8.7	7.6	5.7	10.8	1.6	6.6	4.0
F	16.9	7.5	9.5	4.0	11.9	0.8	7.3	2.4
p	0.54		0.70		0.15		0.37	
Experiment 3								
Treatment								
Control	1.9	2.5	3.2	1.1				
H	2.8	2.8	4.3	0.9				
p	0.30		0.52					

DISCUSSION

The results of the bioassays suggest that *Peltogyne* does not have any allelopathic effect on the germination of the plants. This supports the hypothesis that the *Peltogyne* dominance and the differences found in species composition and species diversity between PRF and FWP are related to other causes.

Although other possible plant organs, such as bark and root, that could be involved in the production of allelopathic compounds were not investigated, the results from experiment 1 (in which litter from beneath *Peltogyne* trees were used) and experiment 2 (in which PRF surface soil were used) did not suggest that this species was producing any allelopathic products.

CONCLUSIONS

Peltogyne did not show any allelopathic effects on the tested plants and its dominance is more likely to be due to other causes.

Chapter 11. Mycorrhizal associations in four important species of the Maracá forests.

INTRODUCTION

The role of mycorrhizae in plant ecology has been reviewed by St. John & Coleman (1983), Newman (1988), Brundrett (1991), Fitter (1991) and Vogt *et al.* (1991). Mycorrhizas are divided into mainly two major types: vesicular-arbuscular mycorrhizas (VAM) and ectomycorrhizas (EM). They are easily distinguished by their morphology and anatomy, VAM have an intracellular hyphae that can form arbuscules and vesicles, while EM have a sheath, which surrounds the host root, and the Hartig net that is formed between root cells (Hudson 1986).

Several authors have pointed out possible ecological roles of these two mycorrhizal types (e.g. Newman 1988, Alexander 1989, Brundett 1991, Vogt *et al.* 1991). VAM and EM are considered to have an important effect in promoting growth of the host by increasing nutrient uptake although there is also evidence that they can affect water relations and pathogen resistance (Parke *et al.* 1983, Davis & Menge 1981 *in* Newman 1988). According to Alexander (1989) the relative efficiency of the two mycorrhizal types in exploiting immobile nutrients, particularly on infertile soils, is not well known, but ectomycorrhizas are assumed to confer special advantages by storing phosphate and water in their sheaths. He also pointed out that EM are, in many cases, associated with single-species dominance or low species diversity. Janos (1983) also suggested that species with an EM association could have a competitive advantage over those with a VAM associations on poor soils and gave several reasons why it should occur.

Connell & Lowman (1989) based on Alexander's (1989) view above cited proposed the "mycorrhiza hypothesis" as a possible mechanism to explain the existence of low-diversity tropical forests. A single tree species with an EM association would gradually achieve dominance basically because it would have a competitive advantage over VAM trees.

The aims of this study were to check whether *Peltogyne gracilipes* and the other three important species of Maracá forests have ectomycorrhizal association and so verify whether *Peltogyne* dominance could be related to the Connell & Lowman's (1989) "mycorrhiza hypothesis".

MATERIALS AND METHODS

ROOT SAMPLING

Roots of *Ecclinusa guianensis, Licania kunthiana, Peltogyne gracilipes and Pradosia surinamensis* (henceforth in this Chapter the species will be referred to by their generic names only) were collected in PRF and FWP by digging along a major root from the base of an identified tree, following the fine branch. Only fine roots (< 2 mm diameter) were collected from three trees ≥ 10 cm dbh of each species. Roots of seedlings of each species were also sampled, but in this case the entire root system was collected.

The roots were placed in plastic bottles and fixed in FAA (13 ml formalin, 5 ml glacial acetic acid, 200 ml 50% ethanol). They were transported to INPA (National Institute of Amazon Research) in Manaus for examination.

PREPARATION OF ROOTS

For the assessment of VA mycorrhizal infection, the roots were cleaned and stained according to the technique described by Philips & Hayman (1970) with the modifications

proposed by Koske & Gemma (1989), while the technique used for rapid assessment of ectomycorrhizal infection was based on Jackson & Mason (1984).

ASSESSMENT OF MYCORRHIZAL INFECTION

The roots were checked only for presence or absence of infection and no quantification of the infection was made.

RESULTS AND DISCUSSION

The microscopic examination of all collections showed that all the study species had VA mycorrhizas. Figures 11.1 and 11.2 show the mycorrhizae of *Peltogyne* and *Licania*. The results are consistent with the findings for other species of *Licania* (St. John 1980a, St. John & Uhl 1983) and *Peltogyne* (St. John 1980b, Alexander 1989). The results reported here for *Pradosia* and *Ecclinusa* seem to be the first records for these species.

Although other important species of Maracá such as *Brosimum lactescens, Lecythis corrugata* and *Tetragastris panamensis* were not examined, previous reports (St. John 1980a and St. John & Uhl 1983) have found VAM associations in their congeners. If the ability to form VA mycorrhizas is assumed to be consistent within a genus, as suggested by St. John (1980b), then those species could be considered likely to be VAM.

The results suggest that on Maracá the VAM type is more common than EM, as has been found for most tree species sampled in the neotropics. Thus, the Connell & Lowman's (1989) "mycorrhiza hypothesis" seems not be supported by this study, since *Peltogyne* is not EM. Alexander (1989) highlighted that although ectomycorrhizal legumes may form low-diversity stands it does not mean that all low-diversity legume stands should be ectomycorrhizal. Martijena & Bullock (1994) also found a VAM species as a dominant tree

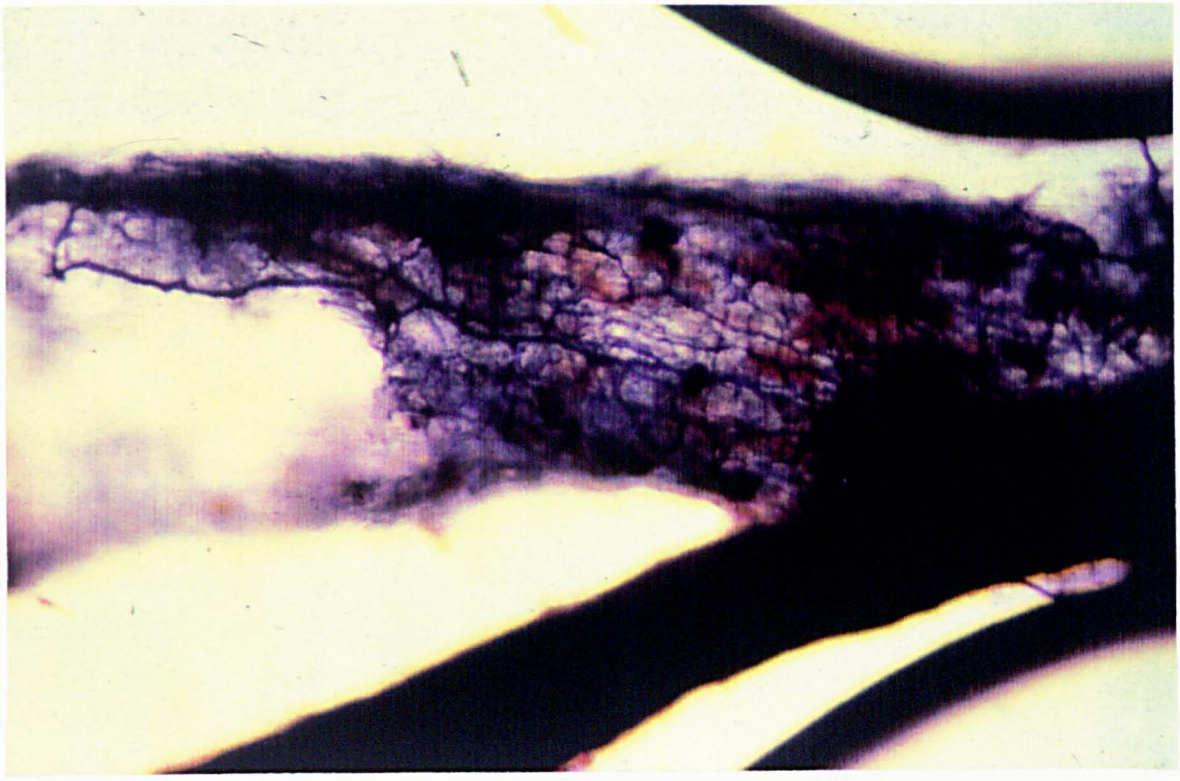

Figure 11.1. Root of *Peltogyne* showing darkly stained hyphae of a VA mycorrhiza.

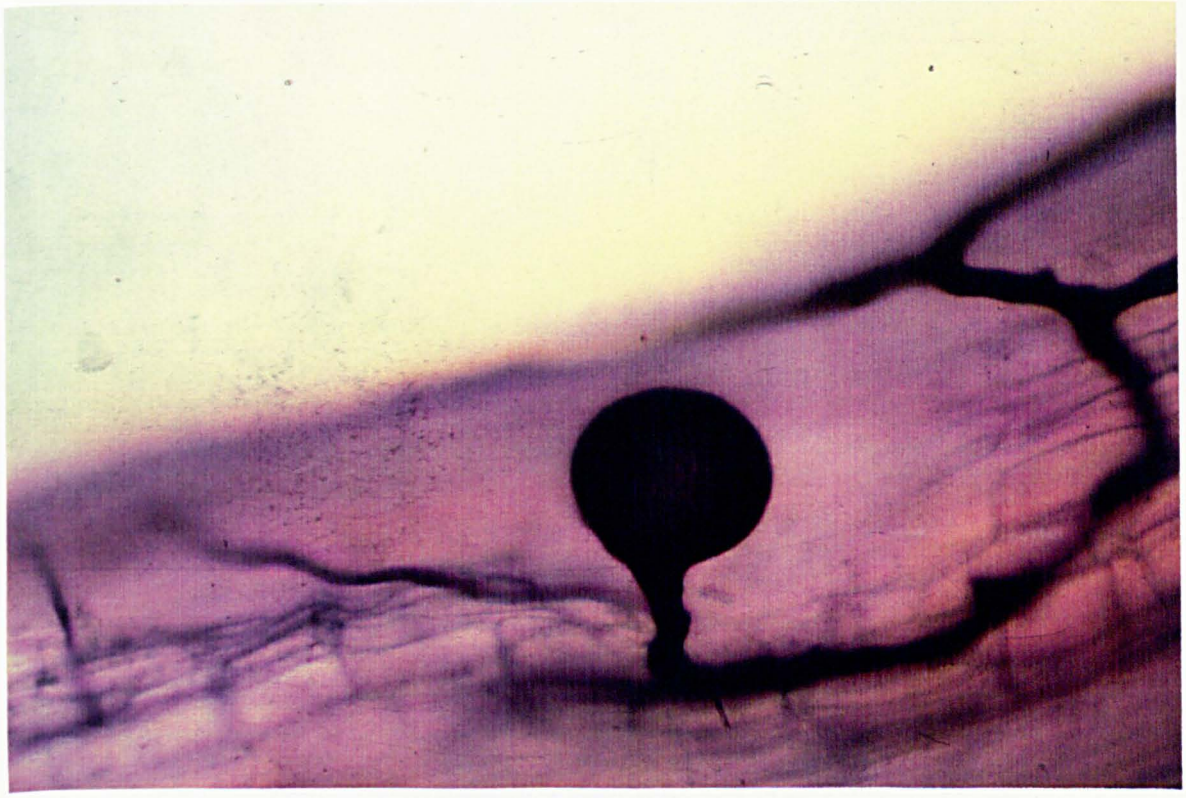

Figure 11.2. Cleared and stained root of *Licania* showing hyphae and a spore of a VA mycorrhiza.

(*Celaenodendron mexicanum*, Euphorbiaceae) in a tropical deciduous dry forest in the Pacific slope of México.

The fungi of VAM are considered to have low specificity (Newman 1988, Alexander 1989). According to Newman (1988) the fungi may link plants. He enumerated some implications for the functioning of ecosystems and provided some evidence that the links influence the species composition and structure of plant communities. One of the pieces of evidence pointed out by him was that "mycorrhizal links could tend to reduce competitive dominance by some plants and hence promote coexistence and species diversity". Again the results here do not support this suggestion, since the *Peltogyne* forest is dominated by a VAM species.

CONCLUSION

The most common species in Maracá forest had VAM, including *Peltogyne*. The dominance of *Peltogyne* seems not be related to mycorrhizal association.

Chapter 12. General discussion and conclusions

FOREST STRUCTURE AND FLORISTICS

The basal area and tree density among forest types are similar, although PRF tends to have higher basal areas and more emergent trees than FWP. The floristics are also similar among forests, especially PRFa, PPF, and FWPa. The ten most important species in each of these forests were almost always represented by the same group of species. Within PRF's, the total species composition is not similar, although *Peltogyne* dominance is. The species composition in PRF is likely to be more related to the forest location on Maracá and so with the surrounding mixed forests. Hart *et al.* (1989) also found this effect for *Gilbertiodendron* forests in central Africa.

It is well known that tropical seral communities (i.e. in early successional stage) may be dominated by a single tree species (e.g. Richards 1952, Nascimento & Cunha 1989, Whitmore 1990), where this species should have characteristics of a pioneer. The regeneration data showed that *Peltogyne* is well established in all size classes and is growing under the closed canopy and is a non-pioneer or climax species (Swaine & Whitmore 1988). Hamilton-Rice (1928) described the *Peltogyne* forest in the Rio Uraricoera as having high numbers of individuals in all size classes. Therefore, PRF has a persistent dominance, falling into type I of the Connell & Lowman's (1989) classification. Other abundant tree species in FWP such as *Ecclinusa guianensis* and *Pradosia surinamensis* are also well represented as tree, seedlings and saplings in PRF. Thus, as found by Hart *et al.* (1989) for a *Gilbertiodendron* forest in central Africa, this study showed that the compensatory mechanisms (Connell *et al.* 1984) do not seem to be affecting the *Peltogyne* dominance in favour of rarer or less common species. The results from the transect analyses reinforced the view that

Peltogyne is advancing into the surrounding forest. Other studies (Marshall 1934, Beard 1946, for *Mora* forest in Trinidad and Hart *et al.* 1989, for a *Gilbertiodendron* forest in Zaïre) have also suggested that these forest types are gradually invading the mixed forest. In all these cases the dominant species have poorly-dispersed seeds, as seems to be the case for *Peltogyne*, indicating that the advance of these species into the adjacent mixed forests might be slow. Hart *et al.* (1989) and Hart (1990) suggested that for a monodominant forest to maintain its dominance or advance into the mixed forest it should be undisturbed in large scale over a long period. Therefore, the disturbance might be the factor that could explain why *Peltogyne*-rich forest is absent from the extreme east of Maracá, since according to Proctor & Miller (1994) the *terra firme* forests from this part of the island are old secondary forests.

Peltogyne DOMINANCE AND PHYSICAL ENVIRONMENTAL

PRF occurs on a wide range of soils from loamy sands to silty clays. Although PRF soils have in general higher concentrations of exchangable cations than FWP, a clear pattern could be observed only for magnesium with the highest Mg/Ca and Mg/total base quotients always found in PRF. Nortcliff & Robison (1989) also found PRF on soils rich in magnesium. According to D. Villela (personal communication) *Peltogyne* has high concentrations of magnesium in its leaves. Thus, the highest concentrations of magnesium in PRF soils might be caused by *Peltogyne* decomposition. However, the soil profile data suggested that the parent material is likely to be the main source of magnesium. Fertilization experiments, using different concentrations of Mg in soils from FWP in the presence of *Peltogyne* and other important species from FWP, are needed to test whether the *Peltogyne* dominance is a result of its adaptation to soils rich in magnesium. The parent-material

source of the magnesium is not known. It is unlikely to be an ultramafic rock (a common source of high magnesium soils) since nickel analyses (not reported in detail) showed low concentrations of this element which invariably accompanies magnesium in these rocks. If the soil Mg determines the *Peltogyne* occurrence and dominance and if the PRF is expanding, as the data in this study suggest, then two possible mechanisms might be involved: the area of Mg-rich soils is still not fully occupied with *Peltogyne* or this species is expanding into low-Mg soils. Further studies are needed to elucidate this question.

According to Robison & Nortcliff (1994) the soils underlying the *Peltogyne* forest are frequently related to poor drainage and damp ground. The study here partially supports this view. As shown in Figure 3.1 PRF seems to follow the drainage system on Maracá. Hamilton-Rice (1928) pointed out that from the mid-east to the west part of the island this forest type is common along the river bank of the Uraricoera. It is important to stress that those areas are not flooded forests, although the water table can reach high levels during the peak of the wet season (D. Villela, personal communication) and some PRF very close to the river bank can be sporadically flooded in years of exceptional rainfall. On the other hand, most of the PRF areas reported by Milliken & Ratter (1989) are on well-drained soil. These data suggest that *Peltogyne* has a wide ecological amplitude and can achieve dominance either on well-drained or wet soils.

***Peltogyne* DOMINANCE AND BIOTIC FACTORS**

SEED PREDATION AND SEEDLING HERBIVORY

According to Janzen (1974) two factors can contribute to species dominance: better defences against seed predators or herbivores through adaptations such as secondary

compounds, or mast fruiting at long intervals that might satiate seed predators. Thus, higher seed and seedling mortality would be expected in species from FWP than in *Peltogyne*. Although there are no comparative data for seed predation between *Peltogyne* and *Licania* or other important species from FWP, the results from this work indicated that seed predation in *Peltogyne* in PRF is not high. However, high levels of seed predation (100%) by ants were observed to occur locally for *Peltogyne* in PPF (Chapter 8). Boucher (1981) found similar results for *Quercus oleoides* in Costa Rica, with this species having 100% predation when occurring in forest where it is not dominant and much lower predation when it is dominant. As pointed by Connell & Lowman (1989), predator satiation seems to enable the species to maintain dominance but not achieve it. Recently, Burkey (1994) suggested that predator satiation is an important factor in the survival of *Brosimum alicastrum* seeds in a tropical forest in México. He found that seed predation increased from the forest edge to the interior. *Peltogyne* seedling mortality was, in most cases, lower than or similar to other common species in PRF and FWP. Therefore, as expected, the abundant regeneration of *Peltogyne* found in the understorey of PRF should be a result of the low seed and seedling mortality in this species. *Peltogyne* does not flower and fruit every year. From 1991 to 1994, this species flowered and fruited only in 1992. During the Maracá project (1987) *Peltogyne* flowered, with voucher specimens being collected (Lewis & Owen 1989). Although no data are available between 1987 and 1991, the data suggest that *Peltogyne* might have a mast fruiting at 2-4 year intervals. Miller (1989) found a 4-year fruiting cycle for *Hymenea parviflora* (Caesalpiniaceae) on Maracá. The *Peltogyne* seeds are poorly dispersed, with most seed falling near to the parent tree. It is in agreement with Hart's (1990) view that dominant species of persistent monodominant forests have poor seed dispersal. Thus, poor seed dispersal coupled to low seed and seedling mortality rates can be considered one of the main

mechanisms for the maintenance of the *Peltogyne* dominance in PRF.

ALLELOPATHY IN *Peltogyne*

Allelopathy can be consider one of the possible mechanisms involved in single-species dominance (Gant & Clebsh 1975, Hart 1990). However, this mechanism does not apparently apply to the *Peltogyne*, since it did not have any allelopathic effect on bioassay plants.

Peltogyne-RICH FOREST AND MYCORRHIZAL ASSOCIATIONS

The Connell & Lowman's (1989) "mycorrhizal hypothesis", seems not to apply to *Peltogyne*, since it has a VAM association and in both PRF and FWP the most important tree species (*Peltogyne* for PRF and *Licania* for FWP) have a VAM association. Therefore, Connell & Lowman's (1989) suggestion that "in forests where the VAM type is more common, most tree species are associated with the same set of fungal species and thus may be nearly equivalent in competitive ability for securing resources. Such equivalence promotes diversity, as suggested by earlier work", is not supported by this study.

GENERAL CONCLUSIONS

1. The *Peltogyne*-rich forest is the least diverse lowland rain forest reported from Amazônia.

2. The *Peltogyne* dominance is related to the magnesium concentration in the soils, especially to the Mg/Ca quotients, which are always higher than 2.

3. *Peltogyne* has a persistent dominance with individuals well represented in all size classes from seedlings to large trees.

4. PRF appears to be gradually expanding, but slowly due to the poorly dispersed seeds and low growth rate of *Peltogyne*.

5. *Peltogyne* trees are prone to occasional high levels of herbivory, mainly when they are undergoing their annual leaf change, but *Peltogyne* seedlings do not suffer mortality due to density-dependent herbivory.

6. The poor seed dispersal in *Peltogyne* together with other life history traits such as tolerance to shade, slow growth rate, low seed and seedling mortality seem to be the mechanisms that explain the maintenance of the dominance of this species in PRF.

7. *Peltogyne* does not have any allelopathic effects.

8. *Peltogyne* has vesicular-arbuscular mycorrhizal associations.

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Appendix 1

A description of each soil pit made in this study is given below.

Plot PRF1 (19 March 1993)- Gently sloping

0-13 cm - Loamy sand 10 YR 4/2 (dark greyish brown), weak fine sub-angular blocky structure, very soft, very frequent fine and medium roots. Very good porosity, with a clear boundary.

13-39 cm - Loamy sand 10YR 5/2 (greyish brown), slightly moderate fine and medium sub-angular blocky structure, soft. Frequent fine roots and medium roots. Good porosity, gradual boundary.

39-86 cm - Loamy sand 10 YR 6/2 (light brownish grey), few mottles 10 YR 7/4 (very pale brown),moderate fine and medium sub-angular blocky structure, slightly hard. Common fine roots. Good porosity, clear boundary.

86-134+ cm - Loamy sand 10 YR 7/1 (light grey), moderate medium to large angular blocky structure, slightly hard. Common fine roots. Good porosity.

Plot PRF2 (18 March 1993)- Gently sloping

0-10 cm - Loamy sand 10 YR 4/2 (dark greyish brown), weak fine sub-angular blocky structure, very soft. Very frequent fine and medium roots. Very good porosity, with a clear boundary.

10-35 cm - Loamy sand 10YR 5/3 (brown), moderate medium sub-angular blocky structure, soft. Common fine and medium roots. Little charcoal at 30 cm depth. Good porosity, gradual boundary.

35-62 cm - Loamy sand 10 YR 6/3 (pale brown), few mottles 7.5 YR 6/6 (light red),moderate medium sub-angular blocky structure, slightly hard. Common fine roots. Good porosity, clear boundary.

62-120+ cm - Loamy sand 10 YR 7/1 (light grey), common mottles 7.5 YR 6/6 (light red), strong moderate large angular blocky structure, slightly hard. Common fine roots. Good porosity.

Plot PRF3 (18 March 1993)- Gently sloping

0-9 cm - Sandy clay loam 10 YR 5/3 (brown), weak fine sub-angular blocky structure, slightly soft, very frequent fine and medium roots. Very good porosity, with a clear boundary.

9-28 cm - Sandy clay loam 10YR 7/4 (very pale brown), moderate medium sub-angular blocky structure, slightly hard. Frequent fine roots and medium roots. Good porosity, gradual boundary.

28-49 cm - Sandy clay 10 YR 7/8 (yellow), moderate medium sub-angular blocky structure, slightly hard. Common fine and medium roots. Charcoal. Good porosity, clear boundary.

49-134+ cm - Clay 2.5 YR 6/8 (light red), common mottles 5 YR 8/2 (pinkish white), strong moderate medium to large sub-angular blocky structure, hard. Very few fine roots. Poor porosity.

Plot PRF5 (from Nortcliff & Robison 1988, Sloth Tapir Pit Ref. 310) very close to Maracá house plot (PRF5).

0-8 cm - A_1 horizon. Silty clay 10 YR 4/3 (brown), strong fine granular, firm, many fine and medium woody roots, high porosity of all sizes, abrupt boundary.

8-28 cm - $A_{2/E}$ horizon. Silty clay 10 YR 5/3 (brown), few mottles 7.5 YR 5/6 (strong brown) along ped surfaces, strong fine subangular blocky, firm, many fine and medium woody roots, high porosity of all sizes, clear boundary.

28-56 cm - B_{t1} horizon. Silty clay (clay) 10 YR 6/4 (light yelowish brown), with few mottles 7.5 YR 5/6 (strong brown) along ped surfaces, moderate medium subangular blocky, firm, common medium and fine woody roots, common small and medium pores, gradual boundary.

56-82 cm -B_{t2} horizon. Clay 10 YR 6/3 (pale brown), common mottles 2.5 YR 4/8 (red) along and through peds, strong moderate subangular blocky, very firm, few fine woody roots, few fine and medium pores, gradual boundary.

82-130+ - B_{t3g} horizon. Clay 2.5 YR 4/6 (red), very common mottles 10 YR 7/3 (very pale brown) and black concretions, moderate coarse subangular blocky, very firm, few fine woody roots, moderate fine and medium pores.

Plot PPF7 (19 March 1993)- Ridge top, flat.

0-15 cm - Loamy sand 10 YR 5/3 (brown), weak fine sub-angular blocky structure, very soft. Very frequent fine and medium roots. Good porosity, with a clear boundary.

15-28 cm - Sandy clay loam 10 YR 6/4 (light yellowish brown), strong moderate medium sub-angular blocky structure, slightly hard. Common fine and medium roots. Good porosity, clear boundary.

28-51 cm - Clay 7.5 YR 8/6 (reddish yellow), strong medium to coarse sub-angular blocky structure, hard. Common fine and few medium roots. Good porosity, clear boundary.

51-141+ cm - Clay 5 YR 6/8 (reddish yellow), very strong large angular blocky structure, hard. Very few fine roots, charcoal?. Poor porosity.

Plot PPF8 (18 March 1993)- Moderately sloping

0-9 cm - Loamy sand 10 YR 4/2 (dark greyish brown), weak fine sub-angular blocky structure, slightly soft. Very frequent fine and medium roots. Very good porosity, with a clear boundary.

9-22 cm - Sand clay loam 10 YR 5/4 (yellowish brown), moderate fine and medium sub-angular blocky structure, slightly hard, common fine and medium roots. Good porosity, gradual boundary.

22-56 cm - Sandy clay 10 YR 6/6 (brownish yellow), strong moderate medium sub-angular blocky structure, slightly hard. Few fine, medium and coarse roots. Good porosity, clear boundary.

56-103+ cm - Clay 7.5 YR 7/8 (reddish yellow) common mottles (2.5 YR 5/6, red), strong large angular blocky structure, hard. Very few fine and medium roots. Poor porosity. Slightly stony with small and medium stones.

Plot PPF9 (18 March 1993)- Gently sloping, much charcoal at 25 cm and 50 cm depth.

0-8 cm - Sandy loam 7.5 YR 4/2 (dark brown), weak fine sub-angular blocky structure, soft. Very frequent fine and medium roots. Very good porosity, with a clear boundary.

8-47 cm - Sandy clay loam 7.5 YR 6/2 (pinkish grey), strong moderate medium sub-angular blocky structure, slightly hard. Common fine and medium roots. Good porosity, clear boundary.

47-135+ cm - Sandy clay 7.5 YR 6/2 (pinkish grey) very many mottles (2.5 YR 6/8, light red), strong large sub-angular blocky structure, hard. Few fine and very few medium roots. Poor porosity, clear boundary.

Plot FWP10 (17 March 1993)- Flat

0-15 cm - Loamy sand 10 YR 4/2 (dark greyish brown), weak fine sub-angular blocky structure, very soft, very frequent fine roots, common roots up to 3 cm. Very good porosity, with a clear boundary.

15-33 cm - Loamy sand 10YR 5/2 (greyish brown), moderate fine and medium sub-angular blocky structure, slightly soft. Frequent fine roots and few medium roots. Good porosity, diffuse boundary.

33-72 cm - Loamy sand 10 YR 6/2 (light brownish grey), strong moderate medium and coarse sub-angular blocky structure, slightly hard. Common fine roots and few medium and coarse roots up to 7 cm, few termite channels. Charcoal, good porosity, clear boundary.

72-148+ cm - Sandy clay loam 10 YR 7/3 (very pale brown), many mottles (7.5 YR 6/6, redish yellow), strong medium to large angular blocky structure, hard. Few fine and medium roots. Good porosity.

Plot FWP11 (19 March 1993)- Flat

0-16 cm - Loamy sand 10 YR 4/2 (dark greyish brown), weak fine sub-angular blocky structure, very soft. Very frequent fine and frequent medium roots. Very good porosity, with a clear boundary.

16-49 cm - Sandy loam 10 YR 5/3 (brown), moderate fine and medium sub-angular blocky structure, slightly soft, frequent fine and medium roots. Good porosity, few charcoal, diffuse boundary.

49-97 cm - Sandy loam 10 YR 6/3 (pale brown), moderate medium sub-angular blocky structure, slightly hard. Common fine and medium roots. Good porosity, clear boundary.

97-140+ cm - Sandy clay loam 10 YR 6/4 (light yellowish brown) common mottles (7.5 YR 7/6, redish yellow), strong moderate coarse angular blocky structure, hard. Few fine roots. Good porosity.

Plot FWP12 (19 March 1993)- Flat

0-15 cm - Loamy sand 10 YR 5/3 (brown), weak fine sub-angular blocky structure, very soft. Very frequent fine and medium roots. Good porosity, with a clear boundary.

15-35 cm - Sandy loam 10 YR 6/3 (pale brown), moderate fine and medium sub-angular blocky structure, slightly soft. Frequent fine and medium roots, few termite channels. Good porosity, diffuse boundary.

35-84 cm - Sandy loam 10 YR 7/3 (very pale brown), moderate medium sub-angular blocky structure, slightly hard. Common fine and medium roots, few termite's channels. Good porosity, clear boundary.

84-146+ cm - Sand clay loam 10 YR 6/4 (light yellowish brown), common mottles (7.5 YR 7/6, redish yellow), strong moderate coarse angular blocky structure, hard. Few fine and medium roots. Good porosity.

Plot FWP13-15 (from Thompson *et al* 1992)

0-20 cm - A horizon. Slightly loamy sand 7.5 YR 3/4 (), coarse weak sub-angular blocky structure breaking to fine, friable peds. Common roots up to 1.5 cm in diameter. Much charcoal, good porosity, with a clear boundary.

20-48 cm - B_1 horizon. Loamy sand 10 YR 5/4 (yellowish brown), coarse moderate sub-angular blocky structure, slightly firm. Frequent roots up to 8 mm in diameter, high porosity, diffuse boundary.

48-82 cm - B_{21} horizon. Sandy loam 7.5 YR 5/6 (strong brown), strong medium to large angular blocky struture. Very firm but some pores up to 1mm in diameter. Some roots up to 3 mm in diameter, diffuse boundary.

82-119+ cm - B_{22} horizon. Sandy clay loam. 7.5 YR 5/6 (strong brown), strong large angular blocky structure. Poor porosity. Very few roots up to 1 mm in diameter.

Appendix 2

List of tree species occurring in the three forest types studied with their codes, authorities and families.

SPECIES CODE	SPECIES	FAMILY	FOREST TYPES		
Abut gra	*Abuta grandifolia* (Mart.) Sandw.	Menispermaceae	PRF	PPF	
Agon sil	*Agonandra silvatica* Ducke	Opiliaceae			FWP
Alex can	*Alexa canaracunensis* Pittier	Fabaceae	PRF		
Alse lon	*Alseis longifolia* Ducke	Rubiaceae	PRF	PPF	FWP
Amai cor	*Amaioua corymbosa* Kunth	Rubiaceae		PPF	FWP
Ampe ede	*Ampelocera edentula* Kuhlm	Ulmaceae		PPF	FWP
Anib hos	*Aniba hostmanniana* (Ness) Mez	Lauraceae			FWP
Apei sch	*Apeiba schomburgkii* Szysz.	Tiliaceae	PRF	PPF	FWP
Arra con	*Arrabidea conjugata* (Vell.) Mart.	Bignoniaceae			FWP
Asco tom	*Ascosmium tomentellum* (Mohl.) Yakovl.	Fabaceae		PPF	
Aspi ete	*Aspidosperma cf. eteanum* Mgf.	Apocynaceae			FWP
Aspi nit	*Aspidosperma nitidum* Benth.	Apocynaceae	PRF	PPF	
Astr acu	*Astrocaryum aculeatum* G.F.W. Mey	Palmae	PRF	PPF	FWP
Astr lec	*Astronium lecointei* Ducke	Anacardiaceae			FWP
Bauh ung	*Bauhinia ungulata* L.	Caesalpiniaceae	PRF		
Bauh sp.	*Bauhinia* sp.	Caesalpiniaceae	PRF		
Bros lac	*Brosimum lactescens* (Moore) C.C. Berg	Moraceae		PPF	FWP
Bros gui	*Brosimum guianensis* Aubl.	Moraceae	TR		
Bros ali	*Brosimum alicastrum* Sw.	Moraceae	TR		
Byrs sch	*Byrsonima schomburgkiana* Benth.	Malpigiaceae			FWP
Case syl	*Casearia sylvestris* Sw. var. *sylvestris*	Flaucortiaceae			FWP
Case ulm	*Casearia ulmifolia* Vahl ex Vent.	Flaucortiaceae	PRF		
Cass mos	*Cassia moschata* Kunth	Mimosaceae			FWP
Clar rac	*Clarisia racemosa* R. & P.	Moraceae			FWP
Cecr sp.	*Cecropia* sp.	Moraceae	TR		FWP
Chau kap	*Chaunochiton kappleri* (Sagot & Egl) Ducke	Olacaceae	PRF		
Chei cog	*Cheiloclinum cognatum* (Miers.)A.C.Smith	Hippocrateaceae		PPF	
Chom bar	*Chomelia barbellata* Standl.	Rubiaceae	PRF	PPF	
Chry arg	*Chrysophyllum argenteum* Jacq.	Sapotaceae		PPF	
Chry spa	*Chrysophyllum sparsiflorum* Kl. ex Miq.	Sapotaceae			FWP
Coch ori	*Cochlospermum orinocense* (Kunth) Steud.	Cochlospermaceae	TR		
Comb sp.	*Combretum* sp.	Combretaceae	PRF		
Cord sel	*Cordia sellowiana* Cham.	Boraginaceae	PRF		
Coue par	*Couepia paraensis* (Mart. & Zucc.) Benth ssp. *glaucescens* (Spr ex Hoor.) Prance	Chrysobalanaceae	PRF	PPF	
Cour mul	*Couratari multiflora* (J.E.Smith) Eyma	Lecythidaceae		PPF	FWP
Cupa sp.	*Cupania* sp.	Sapindaceae			FWP
Crep gou	*Crepidospermum goudotianum* (Tul.)Tr.& Pl.	Burseraceae	PRF	PPF	FWP
Dial gui	*Dialium guianense* (Aubl.) Sandw.	Caesalpiniaceae			FWP
Didy mor	*Didymopanax morototoni* Decne. & Planch.	Araliaceae			FWP
Dryp var	*Drypetes variabilis* Vitt.	Euphorbiaceae	PRF	PPF	FWP
Dugu luc	*Duguetia lucida* Urb	Annonaceae		PPF	FWP
Duro eri	*Duroia eriopila* L.f.	Rubiaceae	PRF	PPF	FWP
Eccl gui	*Ecclinusa guianensis* Eyma	Sapotaceae	PRF	PPF	FWP
Entr sch	*Enterolobium schomburgkii* Benth.	Mimosaceae	PRF	PPF	FWP
Eryt ang	*Erythroxylum anguifugum* Mart.	Erythroxylaceae	PRF		
Esch ped	*Eschweilera pedicellata* (Richard) Mori	Lecythidaceae		PPF	
Euge cup	*Eugenia cupulata* Amsh	Myrtaceae	PRF	PPF	FWP
Euge sp.	*Eugenia* sp.	Myrtaceae	PRF		
Exel bar	*Exellodendron barbatum* (Ducke) Prance	Chrysobalanaceae		PPF	FWP
Fara cra	*Faramea crassiloba* Benth.	Rubiaceae	PRF		FWP
Fara sp1	*Faramea sp.1*	Rubiaceae			FWP
Ficu sp.	*Ficus* sp.	Moraceae	PRF		
Ficu sp1	*Ficus* sp.1	Moraceae	PRF		
Geni ame	*Genipa americana* L.	Rubiaceae	PRF		
Guap sp.	*Guapira* sp.	Nyctaginaceae	TR		
Guat sch	*Guatteria schomburgkiana* Mart.	Annonaceae	PRF	PPF	FWP
Guat sp.	*Guatteria* sp.	Annonaceae			FWP
Guet spr	*Guettarda spruceana* M. Arg.	Rubiaceae			FWP
Gust aug	*Gustavia augusta* L.	Lecythidaceae		PPF	
Hima art	*Himatanthus articulatus* (Vahl) Woods	Apocynaceae	PRF	PPF	FWP
Hirt sp.	*Hirtella* sp.	Chrysobalanaceae	TR		
Hyme cou	*Hymenaea courbaril* L.	Caesalpiniaceae			FWP
Hipp vol	*Hippocratea volubilis* L.	Hippocrateaceae			FWP
Inga bou	*Inga bourgonii* DC.	Mimosaceae	TR		
Inga alb	*Inga alba* Willd	Mimosaceae	TR		
Inga sp1	*Inga* sp.1	Mimosaceae			FWP
Inga sp2	*Inga* sp.2	Mimosaceae	PRF		
Inga sp3	*Inga* sp.3	Mimosaceae		PPF	
Lecy cor	*Lecythis corrugata* Poit.	Lecythidaceae	PRF	PPF	FWP
Lica ape	*Licania apetala* (E.Mey.) Fritsch	Chrysobalanaceae		PPF	
Lica kun	*Licania kunthiana* Hook. F.	Chrysobalanaceae	PRF	PPF	FWP
Lind pal	*Lindackeria paludosa* (Benth.) Gilg.	Flacourtiaceae		PPF	FWP
Lonc sp.	*Lonchocarpus* sp.	Fabaceae	PRF		

Lueh duc	*Lueheopsis duckeana* Bussett	Tiliaceae	PRF	PPF	FWP
Mach sp.	*Machaerium* sp.	Fabaceae	PRF	PPF	FWP
Mach bio	*Machaerium biovulatum* Micheli	Fabaceae	TR		
Mapr gui	*Maprounea guianensis* Aubl.	Euphorbiaceae			FWP
Maur fle	*Mauritia flexuosa* L.F. nc	Palmae	TR		
Maxi mar	*Maximiliana maripa* (Correa) Drude	Palmae	PRF	PPF	FWP
Mayt gui	*Maytenus guianensis* Kl.	Celastraceae			FWP
Mezi ita	*Mezilaurus itauba* (Taub.) ex Mez	Lauraceae		PPF	
Myrc cf.	*Myrcia cf. splendens* (Sw.) DC.	Myrtaceae			FWP
Ocot fas	*Ocotea fasciculata* (Nees) Mez	Lauraceae		PPF	FWP
Ocot san	*Ocotea sandwithii* Kostermans	Lauraceae			FWP
Oeno bac	*Oenocarpus bacaba* Mart.	Palmae		PPF	FWP
Ormo coa	*Ormosia coarotada* Jacks.	Fabaceae			FWP
Ormo smi	*Ormosia smithii* Rudd	Fabaceae			FWP
Ormo sp.	*Ormosia* sp.	Fabaceae			FWP
Ormo sp1	*Ormosia* sp.1	Fabaceae	PRF		
Oura cas	*Ouratea castaneaefolia* (DC.) Egl.	Ochnaceae		PPF	FWP
Pelt gra	*Peltogyne gracilipes* Ducke	Caesalpiniaceae	PRF	PPF	
Pelt pan	*Peltogyne paniculata* (Aubl.) Sandw ssp *pubescens* (Benth.) M.F. da Silva	Caesalpiniaceae	PRF		
Picr cf.	*Picramnia cf. spruceana* Engl.	Simaroubaceae	PRF	PPF	
Pinz cor	*Pinzona coriacea* Mart. & Zucc.	Dilleniaceae	FWP		
Pith sp.	*Pithecellobium* sp.	Mimosaceae	TR		
Pout cla	*Pouteria cladantha* Sandw.	Sapotaceae	PRF	PPF	
Pout his	*Pouteria hispida* Eyma agg.	Sapotaceae	PRF	PPF	FWP
Pout ret	*Pouteria reticulata* (Engl.) Eyma ssp. reticulata	Sapotaceae	PRF	PPF	FWP
Pout sur	*Pouteria surumuensis* Baehni	Sapotaceae	PRF	PPF	FWP
Pout ?	*Pouteria ? torta* (Mart.) Radlk.	Sapotaceae			FWP
Pout ven	*Pouteria venosa* (Mart.) Baehni ssp. amazonica Penn.	Sapotaceae		PPF	FWP
Prad sur	*Pradosia surinamensis* (Eyma) Penn.	Sapotaceae	PRF	PPF	FWP
Prot cre	*Protium crenatum* Sandw.	Burseraceae	TR		
Prot ten	*Protium tenuifolium* (Engl.) Engl. ssp. *tenuifolium*	Burseraceae			FWP
Quii rhy	*Quiina cf. rhytidopus* Tul.	Quiinaceae			FWP
Rino bre	*Rinorea brevipes* (Benth.) Blake	Violaceae	PRF		
Roll exs	*Rollinia exsucca* (Dun.) A. DC.	Annonaceae			FWP
Rudg cra	*Rudgea crassiloba* (Benth.) Rob.	Rubiaceae			FWP
Ryan spe	*Ryania speciosa* Vahl var. *Bicolor* DC.	Flacoutiaceae		PPF	FWP
Sima ama	*Simarouba amara* Aubl.	Simaroubaceae	PRF	PPF	FWP
Sloa gar	*Sloanea garkeana* K. Schum. vel sp. aff.	Elaeocarpaceae			FWP
Sloa gui	*Sloanea guianensis*	Elaeocarpaceae			FWP
Sloa sp.	*Sloanea* sp.	Elaeocarpaceae			FWP
Spon mom	*Spondias mombin* L.	Anacardiaceae	TR		
Swar dip	*Swartzia dipetala* Willd. ex Benth.	Fabaceae			FWP
Swar gra	*Swartzia grandifolia* Bong ex Benth.	Fabaceae	PRF		
Swar lau	*Swartzia laurifolia* Benth.	Fabaceae	TR		
Tabe ule	*Tabebuia uleana* (Kranzl.) Gentry	Bignoniaceae	PRF	PPF	FWP
Tetr pan	*Tetragastris panamensis* (Engl.) Kuntze	Burseraceae		PPF	FWP
Tric cip	*Trichilia cipo* (A.Juss) C.DC.	Meliaceae		PPF	
Tric sp.	*Trichilia* sp.	Meliaceae			FWP
Viro cf.	*Virola cf. sebifera* Aubl.	Myristicaceae	TR		FWP
Vite sch	*Vitex schomburgkiana* Schaver	Verbenaceae	PRF		
Xant aff.	*Xanthoxylum aff. rigidum* H. & B.	Rutaceae	PRF		
Xylo fru	*Xylopia frutescens* Aubl.	Annonaceae			FWP
Zoll gra	*Zollernia grandifolia* Schery	Fabaceae	PRF		
Zygi sp1	*Zygia* sp.1	Mimosaceae	PRF		
Zygi sp2	*Zygia* sp.2	Mimosaceae	PRF		
DS 177	DS 177				FWP
DS 180	DS 180				FWP
DS 210	DS 210				FWP
DS 453	DS 453	Rubiaceae			FWP
DS 535	DS 535				FWP
DS 628	DS 628				FWP
MTN 17	MTN 17		PRF		
MTN 224	MTN 224		PRF		
MTN 225	MTN 225		PRF		
MTN 342	MTN 342		PRF		
MTN 389	MTN 389,433		PRF		
MTN 414	MTN 414		PRF		
MTN 279	MTN 2791		TR		
MTN 284	MTN 2847		TR		
MTN 286	MTN 2864		TR		
MTN 287	MTN 2876		TR		
MTN 314	MTN 3141				FWP
MTN 349	MTN 3499			PPF	
MTN 383	MTN 3834	Rubiaceae	PRF		
MTN 392	MTN 3923		PRF	PPF	FWP
MTN 373	MTN 3733		PRF	PPF	
MTN 397	MTN 3973		PRF		
R 564	R 5645				FWP

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Appendix 3

INSECT DEFOLIATION OF A MONODOMINANT AMAZONIAN RAIN FOREST

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A rain forest type dominated by the leguminous (Caesalpiniaceae) tree Peltogyne gracilipes Ducke was recently discovered (Milliken & Ratter 1989) on Maracá Island, Roraima, Brazil (3° 20' N, 61°20' W). The forest type is apparently primary and has an area of several square kilometres both on the island and on the mainland to the south. Monodominant rain forests are rare in the wet tropics and the Peltogyne forest is the first recorded from Amazônia. On Maracá the Peltogyne forest forms strips, each up to several hundred hectares in area, which are conspicuous in the later part of the dry season when, from December to early April, many of the larger trees are leafless. During the course of investigations on the causes of the Peltogyne monodominance a remarkable herbivory event was recorded.

On 9 April 1992 the first evidence of an infestation, the noise of larvae chewing the leaves, was heard. It was rapidly realized that the infestation was widespread over the Peltogyne forests of Maracá Island and some aspects of it were recorded in detail. All Peltogyne trees (≥ 10 cm diameter at breast height) in three 50 m x 50 m plots (1-3) where the species was monodominant were checked on 14-16 April 1992. At the same time, using the same methods, the extent of the herbivory was compared in three similar plots (4-6) where Peltogyne was represented by a few individual trees but not monodominant. The

trees were undergoing their annual leaf change at the time of the attack. Some were bare, having abscised their old leaves and not yet produced new ones, some had no new leaves but had retained their old leaves, others were producing new leaves and retained a varying amount of the old foliage. For each individual tree the phenological state was recorded along with herbivore damage: no damage; low damage (up to 25% of the crown defoliated); moderate damage (25-50%); heavy damage (50-90%); and extreme damage (> 90%). (Trees with extreme damage were easy to distinguish from those that had simply shed their leaves since the former retained large numbers of uneaten petioles). Large numbers of Peltogyne saplings and seedlings were also investigated in the same way in sub-plots within each plot.

A rough estimate of the number of pupae per plot was rapidly obtained from quadrats placed in a stratified random manner in each plot. The pupae were counted from the litter layer and soil surface. They were reared until they hatched and the adults were identified as Eulepidotis phrygionia Hampson, a generalist moth of the Noctuidae that is widespread in Brazil (V. Becker personal communication).

The results of the Peltogyne damage survey and pupal count are shown in Table 1. The severity of the attack was greatest in plots 1 and 2 which had the highest number of pupae. Only trees with new leaves were attacked by E. phrygionia and plot 3 with few trees with new leaves was less badly damaged. Plot 6 had no trees with new leaves and no E. phrygionia damage. Saplings and seedlings had no new leaves and their existing foliage was never observed to be eaten by the larvae. Virtually all trees with new leaves were attacked in each plot.

A second infestation of the same species of moth occurred and was first observed on 24 April 1992 and lasted for 6 days. It was less severe than the first infestation except

in Plots 3 and 6 which had produced a considerable leaf flush by the time of the second infestation.

By early June 1992 all the mature trees which had been defoliated had produced a second flush of leaves and were flowering. A survey of Peltogyne leaves collected from litterfall traps over the year before infestation had shown that in the forest where there were few individuals of Peltogyne, the litterfall leaves of this species had a mean of 16.6% of their area removed by invertebrate herbivores before they fell. The corresponding value for the Peltogyne-rich forest was 11.4%. These two values were not significantly different, and are similar to an overall value of 11.3% (Scott 1990) for leaf hole area in litterfall leaves of a range of species in species-rich forest (Thompson et al 1992) about 3 km distant from the Peltogyne forest. These values for herbivory seem to reflect a background level of mature leaf consumption which is unrelated to the infestation of new leaves.

There have been many reports of severe defoliation of tree species in tropical forests (e.g. Janzen 1981,1984; Wolda & Foster 1978; and Wong et al. 1990). However, the mass defoliation of Peltogyne is perhaps the first such instance which has been fully observed in a monodominant tropical forest type. Large-scale deaths of the gregarious tree Shorea albida were reported (Anderson 1961) in peat swamps and heath forest in Sarawak and Brunei. They were attributed mainly to an unidentified lepidopteran larva which was not seen, but only assumed to exist from local reports. It is odd that the Shorea albida died after the presumed attacks but it was suggested (Anderson 1961) that it seemed to be sensitive to damage, possibly because the whole ecosystem was becoming less favourable for it.

It is noteworthy that the observations of Wong et al. (1990) on the defoliation of Quararibea asterolepis (Bombacaceae) on Barro Colorado Island, Panama, involved two

undentified moth species of the same genus (Eulepidotis) as that in the present study. There were several similarities between their observations and these on the Peltogyne including the restriction of larval attacks to young leaves. The observations that the young leaves of Peltogyne were eaten is in agreement with others (Lieberman & Lieberman 1984; Ernest 1990; Kursar & Coley 1992) which have been made on other species concerning the decrease in palatability with leaf age. However the extent of the defoliation observed here suggests that it is wrong to suppose (Aide 1988; Aide & Londoño 1989) that the strategy of simultaneous leaf flushing has evolved to satiate herbivores in tropical forests and hence reduce their damage. It would appear that E. phrygionia herbivores are not satiated by a super-abundant food resource but can produce large populations quickly in response to it.

The events of 1992 were not repeated in 1993 when a different leaf phenology pattern prevailed. By mid-March (before the beginning of the wet season) about 50% of the Peltogyne trees were flushing new leaves but most of the trees retained at least half of their old leaves. No extensive herbivory was observed on the new leaves, possibly because their earlier production in 1993 avoided a wet season abundance of herbivores. Late dry-season leaf production has been shown to reduce herbivory elsewhere (Nascimento, Villela & Lacerda 1990; Aide 1992) but the causes of the different timings of Peltogyne leaf production between 1992 and 1993 are unknown.

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TABLE 1. The percentage of individual trees (≥ 10 cm dbh) of Peltogyne gracilipes in five defoliation classes in three 50 m x 50 m plots in each of (a) forest where the species was dominant; and (b) forest where it had few individuals. The mean number of pupae of Eulepidotis phrygionia, estimated from three 30 cm x 30 cm quadrats in each plot, is also given. n = the number of Peltogyne trees.

			Defoliation					
	Plot No.	(n)	0%	<25%	25-50%	50-90%	>90%	Pupae (m^{-2}±SE)
(a)	1	28	43	0	0	29	29	119±132
	2	28	36	0	0	36	29	100±29
	3	21	67	0	19	10	5	11±11
(b)								
	4	7	14	0	0	86	0	44±29
	5	6	17	50	33	0	0	3.7±6.4
	6	6	100	0	0	0	0	0